FROM ROUTES, NON-BREEDING SITES AND TIMING TO REPRODUCTIVE SUCCESS – MIGRATION PATTERNS IN HOOPOES AND WRYNECKS

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From Routes, Non-breeding Sites and Timing to Reproductive Success – Migration Patterns in Hoopoes and Wrynecks

PhD Thesis

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SUMMARY

The annual cycle of migrating birds encompasses many perils and obstacles, but it allows birds to avoid food scarcity during winters, which is common when breeding grounds are influenced by a temperate climate. Migration is thus beneficial for survival, but it may also incur fitness costs. For example, it can influence current reproductive success. To better understand the population dynamics of migrants and for their proper conservation, it is crucial to study their complete annual cycle: migration routes, timing, non-breeding sites, but also potential consequences on reproductive success. In this thesis, I studied these aspects in Hoopoes *Upupa epops* and Wrynecks *Jynx torquilla* using geolocators that were deployed between 2010-2015 on individuals of breeding populations in Southern Switzerland (Valais) and likewise used data on breeding phenology for the same time span.

In order to investigate the migratory behaviour of individual birds, devices have to be used to keep track of their whereabouts. Non-invasive techniques exist, such as stable isotopes, but these techniques only give relatively poor and coarse information on the whereabouts of an individual. The use of e.g. geolocators can give more precise information, but may lead to a change in behaviour and thus also might affect migration patterns. I show in chapter 2 using an extensive set of investigated parameters, ranging from fledgling weight to apparent annual survival, that Hoopoes were not affected by carrying a geolocator with a weight corresponding to <2% of their body mass. I conclude that with the proper design and an as low as possible relative weight of a device, they can be used and give invaluable insights into detailed migratory behaviour of an individual.

One aspect that is key to the understanding of population dynamics, also in the light of conservation, is where birds spend the wintering (non-breeding) season. Contrary to previous believes I show that Wrynecks from Central-European populations are short-distance migrants wintering in Northern Africa and on the Iberian Peninsula (chapter 3). Similar to their breeding grounds they prefer agricultural habitat with shrubs/orchards and patches of open, sandy soil where they can forage on ants, their main food source (chapter 4). Both findings have implications for understanding the mechanisms behind population dynamics of not only Wrynecks, but also other migrants, since reasons might have to be sought elsewhere than assumed to date.

Whether birds are able to temporally compensate for delays in their annual routine imposed e.g. by environmental impact and if so, to which degree, is still largely unknown. I found that hoopoes are able to compensate at least during parts of the annual cycle for ‘mistiming’ (chapter 5). Most notably the post-breeding and wintering period allowed for compensation of a late departure by decreasing the duration between the start and finish of these periods. During the pre-breeding period, birds can hardly compensate, meaning that a late arrival will lead to a later onset of

breeding, which in turn leads to a slight decrease in reproductive success. Thus even though birds can compensate their timing to some extent, there is a penalty at the final stage of migration, where spring migration determines arrival and in turn reproductive success.

Besides temporal flexibility, bird migration is also characterised by spatial flexibility, both of which result in a degree of individual repeatability of migratory behaviour. As I show in chapter 6, hoopoes followed the same general autumn migration directions and migrated to a similar wintering region each year, but often changed the exact wintering location and thus wintering site fidelity appears to be low. Also autumn migration timing was repeatable in both groups, contrary to spring migration. I argue that this shows that hoopoes are migrants with a high breeding site fidelity, but a relatively opportunistic behaviour outside the breeding season, perhaps profiting from very specific local conditions (e.g. wadis) and food resources (e.g. locust outbreaks).

As these last two chapters show, migration might be less rigid as has been thought to date. In that respect, it is not surprising that current breeding success is affected predominantly by the previous breeding success, but only to a much lesser extent by events happening on migration (chapter 7). This suggests that the intrinsic quality of individuals plays an important role. We conclude that spring migration may influence the variation in breeding success, but that the intrinsic quality of an individual is more important to actually reproduce by gaining and defending the best territories, providing sufficient food for nestlings and maintaining the individual's condition, thereby increasing changes of survival.

Overall, hoopoes show a remarkable resilience during migration, adapting *en route* and in the wintering sites, both on a temporal and spatial level. Where exactly they go and which conditions are preferable, is still a black box since hardly any data is available on the exact locations of their non-breeding sites and how these relate with the dietary preferences of hoopoes (and many other migrants) in their wintering sites. Future research thus should focus on a better understanding of what happens on site during the non-breeding season and how birds prepare for the return migration to the breeding grounds. Clearly, there are advantages of departing in good condition and arriving early, but the exact mechanisms and the variation between individuals, are still poorly understood.

ZUSAMMENFASSUNG

Jahreszeitliche Schwankungen der Umwelt stellen Vögel vor grosse Herausforderungen, z.B. Nahrungsmittelknappheit im Winter. Zugvögel meistern diese Herausforderung in dem sie in den Süden ziehen. Damit erhöhen sie ihre Überlebenswahrscheinlichkeit während des Winters. Es ist jedoch nicht auszuschliessen, dass die Reise auch negative Auswirkungen für die Fitness hat, die sich dann zu einem anderen Zeitpunkt im Jahr zeigt. Um die Populationsdynamik von Zugvögeln besser zu verstehen und sie besser schützen zu können, ist es also notwendig, denn ganze Jahreszyklus zu studieren: Zugrouten, "Timing", Lage der Wintergebiete, aber auch potenzielle später auftretende Konsequenzen auf Bruterfolg. In meiner Dissertation untersuchte ich diese Aspekte für Wiedehopfe (*Upupa epops*) und Wendehalse (*Jynx torquilla*) in der Schweiz in einer walliser Population. Ich verwendete Brutdaten und kombinierte sie mit Geodatenloggern Daten für die Jahre 2010-2015.

Um das Migrationsverhalten von individuelle Vogel zu untersuchen, ist es notwendig technische Instrumente zur Verfolgung zu benutzen. Zwar existieren bereits non-invasive Methode, zum Beispiel stabile Isotope, aber diese haben nur eine sehr ungenaue räumliche und zeitliche Auflösung. Ich verwendete deshalb für meine Studie Geodatenloggern, aber diese stellen für den Vogel einen zusätzlichen Luftwiderstand und ein zusätzliches Gewicht dar, was möglicherweise zu Änderungen im Verhalten, insbesondere im Migrationsverhalten, führen könnte. In Kapitel 2 zeige ich an Hand einer Vielzahl von untersuchten Variablen, dass Wiedehopfe von Geodatenloggern, < 2% ihres Körpergewichtes, nicht beeinflusst werden. Ich schliesse daraus, dass wann die Bauart und das Gewicht von Geodatenloggern sorgfältig gewählt werden, wir diese Instrumente verwenden können um wertvolle Einblicke in das Migrationsverhalten individueller Vögel geben zu können.

Ein wichtiger Aspekt der Populationsdynamik von Zugvögeln, auch für Naturschutzzwecke, ist zu wissen wo die Vögel ihre Zeit ausserhalb der Brutsaison verbringen. Ich konnte zeigen, dass entgegen der bisherigen Lehrmeinung, Wendehalse von zentraleuropäischen Brutpopulationen in Nordafrika und auf der iberischen Halbinsel überwintern und nicht in Afrika südlich der Sahara. Sie sind also nur Kurzstreckenzieher (Kapitel 3). Als Habitat im Winter scheinen sie die gleichen Bedingungen wie im Brutgebiet zu bevorzugen: landwirtschaftlich genutzte Landschaften durchsetzt mit Gebüschen und offenen, sandigen Flächen wo sie Nahrung (Ameisen) suchen können (Kapitel 4). Solche Ergebnisse zeigen auf wie wichtig eine präzise Lokalisierung der Überwinterungsgebiete von Zugvögeln ist, weil nur so Gründe ausserhalb der Brutgebiete für Erklärungen zu Populationsrückgang herangezogen werden können.

Ob Zugvögel sich an Änderungen in ihre Umgebung, zum Beispiel an den Klimawandel, anpassen können und wann ja, in wie weit, wurde bis jetzt noch kaum untersucht. Für Wiedehopfe scheint es

tatsächlich Perioden während des Jahresverlaufs zu geben, die die Vögel flexible verkürzen können um damit Artgenossen im Jahreszyklus zeitlich aufzuholen (Kapitel 5). Ich fand, dass Wiedehopfe sowohl in der Periode nach der Brutsaison, in der Überwinterungsperiode als auch geringerem Umfang während des Herbst- und Frühlingszug Zeit kompensieren können. Jedoch können Vögel nach der Ankunft im Brutgebiet kaum noch verlorene Zeit aufholen und eine späte Ankunft bedeutet dann meistens auch einen späten Anfang der Brut, was wiederum zu einem geringeren Bruterfolg führt. Die Periode unmittelbar vor der Ankunft ist also die Entschiedenste im gesamten Jahreszyklus für einen hohen Bruterfolg.

Wiedehopfe unterscheiden sich individuell sowohl zeitlich wie auch in der Routenwahl in ihrem Zugverhalten, selbst innerhalb des Individuums. In Kapitel 6 zeige ich, dass die Ortstreue im Überwinterungsgebiet sowohl für erstmals ziehende sub-Adulte als auch für erwachsene Wiedehopfe gering ist. Individuen folgten aber mehr oder weniger Jahr für Jahr den gleichen Zugwegen zu ihren Überwinterungsgebieten. Das Timing im Herbst war wiederholbar im Gegensatz zu dem Timing in Frühling. Ich argumentiere das Wiedehopfe Zugvögel mit einer hohen Ortstreue im Brutgebiet sind, aber ein opportunistisches Verhalten ausserhalb das Brutgebiets zeigen und dabei vielleicht sehr geschickt spezifische Umweltbedingungen (wie Wadis) und Futterquellen (wie Heuschrecken Ausbruche) auszunutzen wissen.

Wie diese letzten zwei Kapitel zeigen, ist Migrationsverhalten vielleicht weniger statisch wie bisher angenommen. Den grössten ‘carry-over’ Effekte fanden wir von dem vorherigen zu dem aktuellen Bruterfolg, während Timing des Zuges, Migrationsverhalten und die generellen Winterbedingungen nur wenig der Varianz des Bruterfolgs erklären konnten (Kapitel 7). Wir schliessen daraus, dass obwohl ins besondere der Frühlingszug den Bruterfolg massgeblich beeinflusst, die intrinsische Qualität des Individuums wichtiger ist. Und diese Qualität wird wahrscheinlich viel mehr dadurch festgelegt, ob ein Individuum tatsächlich zum Brüten kommt, ein gutes Territorium besetzen und verteidigen kann, genügend Futter für die Jungvögel sammeln kann und ob die Körperkondition zum Überleben ausreichen, als welche Zugstrategie es wählt.

Als Schlussfolgerung stell ich fest, dass Wiedehopfe eine aussergewöhnliche Flexibilität ausserhalb des Brutgebietes - sowohl unterwegs als auch in ihrem Wintergebiete - besitzen und sich sowohl zeitlich wie räumlich den Variablen Umweltbedingungen anpassen können. Leider zeigte sich aber auch, dass für eine noch genauere Beschreibung der Habitatswahl innerhalb dieses Gebietes, zum Beispiel über die Futterpräferenzen und das Sozialesverhalten, die Geodatenloggern eine zu ungenaue Positionierung der Vögel erlauben.

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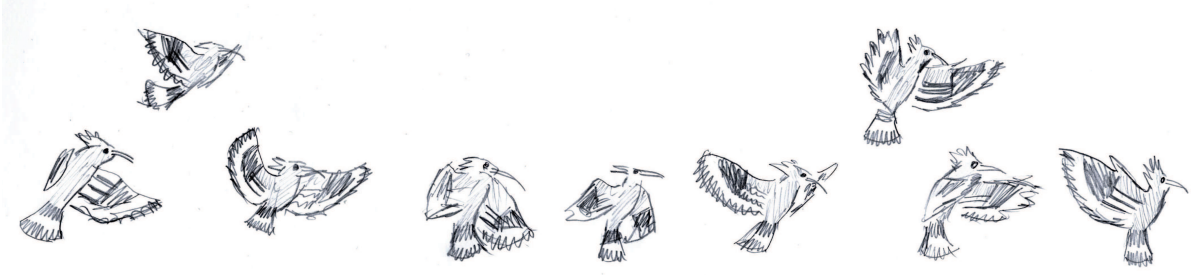

CHAPTER 1 – GENERAL INTRODUCTION

Migration is a widespread phenomenon across taxa, and is especially well studied in birds, where it is defined as the seasonal movement between the breeding and wintering (non-breeding) grounds (Berthold 2001).

Migration is an energy-demanding activity, which migrating birds have to incorporate next to other energy demanding activities such as breeding and moult. In addition, all these activities take place at multiple distant sites at particular times during the year (McNamara et al. 1998, Newton 2008, Barta et al. 2008, Gilg and Yoccoz 2010). Migration allows individuals to move between these activities to exploit and profit from resources that are available only at certain times and places during the year. Given this spatio-temporal variability in resources, some periods are better suited for particular activities compared to others (Drent 2006, Newton 2008, Barta et al. 2008). For example during the boreal winter, there is not sufficient food for birds to breed and they can better spend the winter in warmer regions instead. Therefore, the timing of activities and the conditions of the sites visited are widely considered to have significant fitness consequences on an individual level, which can lead to changes in the demographic rates of a population (Berthold 2001, Newton 2006, Møller et al. 2008).

Optimal tracking of resources throughout the year enables birds to proceed swiftly with migration, complete moult, and have a successful breeding season (Egevang et al. 2010, Alerstam 2011, van Wijk et al. 2012). Penalties for not starting activities at the optimal time may range from slight reductions in reproductive success (fewer fledglings or fledglings with lower survival prospects, Lepage and Gauthier 2000, Gienapp and Bregnballe 2012) to fatal consequences such as starvation caused by mistiming of migration (Piersma 2007). Furthermore, birds have to adapt to climate changes that differ in magnitude and direction between the breeding and wintering grounds and stopovers along the way (Gordo et al. 2005, Both and te Marvelde 2007). The timing of the annual cycle in migrating birds thus is a very challenging and complex task.

In some ways birds can ‘improve’ their timing with increasing age or adapt to new breeding and wintering sites in order to optimally profit from the stochastic environment they move around in during the year, but such repeatability within an individual has hardly been studied to date and it is thus difficult to make predictions how flexible migrating birds can be. They are faced with multiple sites during the year each with their own phenology and as such specific periods with favourable conditions and peak resource availabilities. Conditions thus need to be forecasted at distant sites, possibly far into the future. The conditions experienced at the current site are thus a result of decisions made on previous sites. For example, the winter habitat quality has been shown to affect

the timing of and condition during subsequent spring migration (Paxton and Moore 2015, Cooper et al. 2015). Likewise, the date of arrival and the body condition upon arrival in the breeding grounds are both crucial to optimize reproductive success (Kokko 1999, Drent et al. 2003, Newton 2006, Verhulst and Nilsson 2008). Arriving too late may come at a cost, but also arriving too early may bear the risk of experiencing adverse weather conditions and thus the risk of starvation (Boyd and Piersma 2001). Arrival in the breeding grounds and body condition at arrival likely depend on earlier behaviour and experiences elsewhere, e.g. the departure from, and conditions in, the wintering sites (Schaub et al. 2005, Newton 2006, Robson and Barriocanal 2011, Ockendon et al. 2014, Paxton and Moore 2015, Cooper et al. 2015). This in turn depends on e.g. the date of arrival in the wintering grounds, which in turn could depend on the date of departure from the breeding grounds and so on. Such so called carry-over effects can have a profound impact on the individual's fitness (Nilsson and Svensson 1996, Inger et al. 2010, Harrison et al. 2011), but to date they have hardly been addressed in bird migration studies. A great scientific challenge thus lies in understanding exactly "how events at any one stage of the migratory cycle affect other stages …", including on reproduction (Wilcove and Wikelski 2008) and "the decision rules by which migratory animals determine where to go, how long to stay, and when to leave" (Piersma 2007, Wilcove and Wikelski 2008, Bauer et al. 2011). In order to increase our understanding of migration and its effects on individual fitness, we thus need to study annual routines; complete annual cycles and the effect of different migration strategies on the individual's reproductive success and fitness (McNamara et al. 1998, Drent et al. 2003, Webster and Marra 2005, McNamara and Houston 2008, Marra et al. 2015, Hostetler et al. 2015).

The study of annual routines requires data of all successive events from breeding through migration to the wintering grounds and back to the breeding grounds. Obtaining migration data is a difficult task, especially in smaller birds. Even though recently major improvements have been made towards miniaturizing satellite and GPS tags, these are still not light enough for the majority of migrating birds (Bridge et al. 2011). Indirect tracking methods such as stable isotopes (Hobson et al. 2004, Procházka et al. 2007, Hobson 2011, Franks et al. 2012), genetics (Pulido et al. 2001, Webster et al. 2002, Pérez-Tris et al. 2004, Pulido 2007) and ringing (Bairlein 2001), have yielded first insights in the migratory behaviour in many systems, but these methods still lack the spatial and temporal resolution needed to investigate complete annual cycles, including the effect of migration on reproductive success and vice versa.

Only very recently a new device has found its way into bird migration research: light level loggers or so called geolocators. Geolocators register the intensity of light over time which allows for an estimation of the latitude (day or night length) and longitude (time of mid-day or mid-night). Even though they have been introduced in marine mammal research already a few decades ago (Hill

1994), it was not until recently that they were miniaturized so that they could be used on (small) birds (Stutchbury et al. 2009, Egevang et al. 2010). This has opened up a whole new field of research and drastically increased the number of studies on the migratory behaviour of species with body weights down to 15 grams (Bridge et al. 2013, Ouwehand et al. 2015). The method has its drawbacks though, most notably the relatively low accuracy of position estimates (Lisovski et al. 2012, Fudickar et al. 2012). Additionally, during the equinoxes in September and March when day length is the same all around the globe, latitude positions cannot be calculated (Hill 1994, but see Rakhimberdiev et al. 2015). Furthermore, the added weight and drag of the geolocator could negatively affect an individual's (migratory) behaviour (Barron et al. 2010, Costantini and Møller 2013). The general rule of thumb states that the relative weight of a device put on a bird should not exceed five percent (Kenward 2001), but it has been suggested that this preferably should be less than three percent (Vandenabeele et al. 2012). The potential negative effect of the device on an individual should always be investigated to be confident that the manipulated individuals are representative of the population.

Taking these limitations into account, the use of geolocators allows for identification of approximate wintering sites and migration routes & timing of many small birds. It has already yielded many remarkable results e.g. where birds are wintering, which can be a start for habitat use studies in winter which are very scarce to date. For instance, it has always been assumed that Bluethroats (*Luscinia svecica*) from Norway were wintering in eastern Africa. It was shown only very recently that they actually winter in India (Lislevand et al. 2015). Such findings not only have a scientific impact, but also are of major importance to a proper conservation management, since populations of long-distance migrating birds are declining throughout Eurasia (Sanderson et al. 2006, Walther et al. 2011) and reasons for these declines thus may have to be looked for elsewhere. Geolocators have also made it possible to investigate migration routes and wintering sites of different populations of the same species, which has boosted our understanding whether birds of the same breeding grounds also winter in the same wintering grounds, i.e. how strong the migratory connectivity is of a focal species. Studying migratory connectivity is important, since a population with high migratory connectivity, i.e. using the same breeding and wintering grounds each year, will be much more vulnerable to environmental and climate changes (Webster and Marra 2005, Salewski et al. 2012). Migratory connectivity has always been assumed to be high, but actually in an increasing amount of species, it has been shown that individuals of the same population spread out over huge areas in winter, to return to the same breeding grounds again the next year (Lemke et al. 2013, Cano and Tellería 2013).

There are thus still a lot of open questions as to how birds time their migration, where they go in winter and how they get there and how this subsequently affects their reproductive success. In turn their reproductive behaviour might have an influence on the subsequent migration, which again can influence reproductive success and this process may be repeated multiple times. Disentangling the annual cycle and quantifying the effects of each event is a major challenge and one that has not been tackled often to date, especially in small birds. Given major declines in populations of many of these migrating species, it is apparent that a better understanding of the annual cycle can greatly enhance our knowledge on why such species are declining and what the most crucial stages are during the year.

Study species and study site

This thesis focuses on the annual cycle of two migrating birds: the Eurasian Hoopoe (*Upupa epops epops*) and the Eurasian Wryneck (*Jynx torquilla*). Both species are secondary cavity breeding near-passerines and most populations are migratory (Cramp et al. 1985). They occur in semi-open to open landscapes such as orchards, vineyards, small woods, etc. Hoopoes are specialized foragers feeding on (soil) invertebrates (Bauer et al. 2005), whereas Wrynecks almost exclusively feed on ants (Mermod et al. 2009). Populations of Hoopoes have undergone dramatic local declines all across Europe in the 20th century (Arlettaz et al. 2000), mainly for reasons that are directly or indirectly related to changes in the agricultural landscape (e.g. replacing high stem fruit trees by dwarf fruit trees). In Switzerland the Hoopoe was widely distributed in the 1950s, but nowadays they are restricted mostly to the southwestern part (canton of Valais), with some remaining breeding pairs in the cantons Grisons and Ticino (Arlettaz et al. 2000). It is listed on the Red List of Switzerland as “endangered” (Keller et al. 2010) and it is included in a list with 50 priority species of special conservation interest (Swiss Ornithological Institute). As a consequence, in collaboration with the University of Bern, ~700 nestboxes were installed around the turn of the 21st century in the Rhône valley in the canton of Valais as a conservation measure to decrease the distance between foraging areas in the valley and breeding sites which up till then where mainly located further away on the slopes. The area extends from Vernayaz (450m asl) to Sierre (520m asl) over a total area of roughly 62km^2 (Fig. 1) and is dominated by intensive agriculture consisting mainly of dwarf fruit tree plantations and vineyards (Fig. 2). The installation of the nestboxes indeed led to a rapid increase of the Hoopoe population (Arlettaz et al. 2010a, Berthier et al. 2012) and additionally Wrynecks started using the nestboxes.

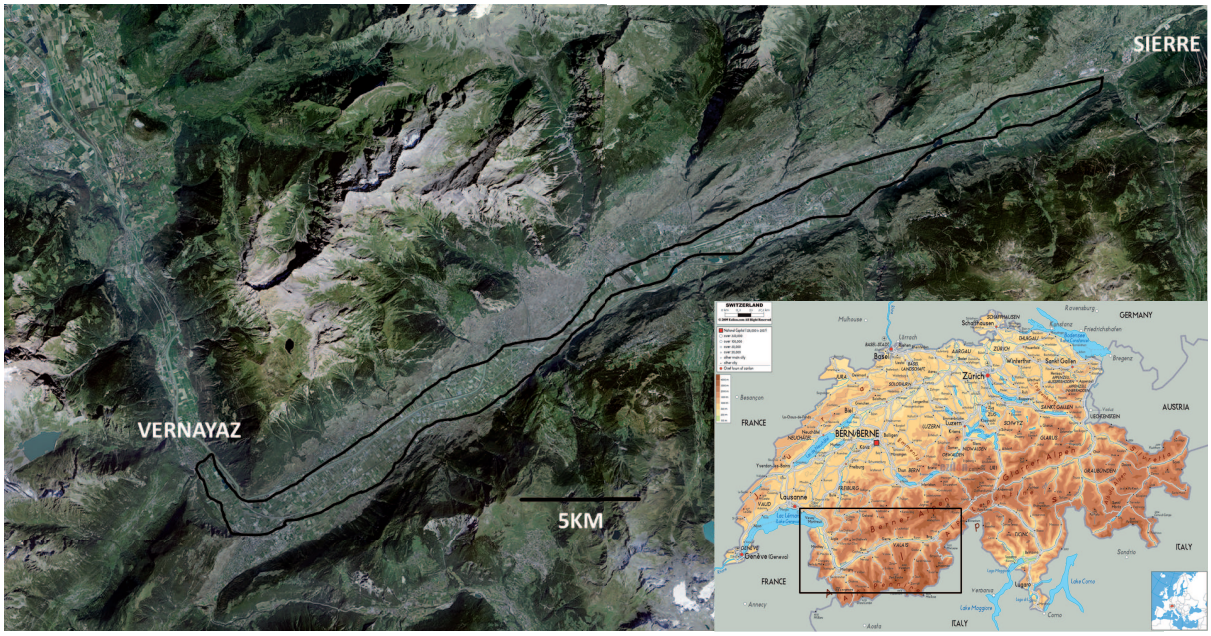

Figure 1. Location of the study area, outlined in black.

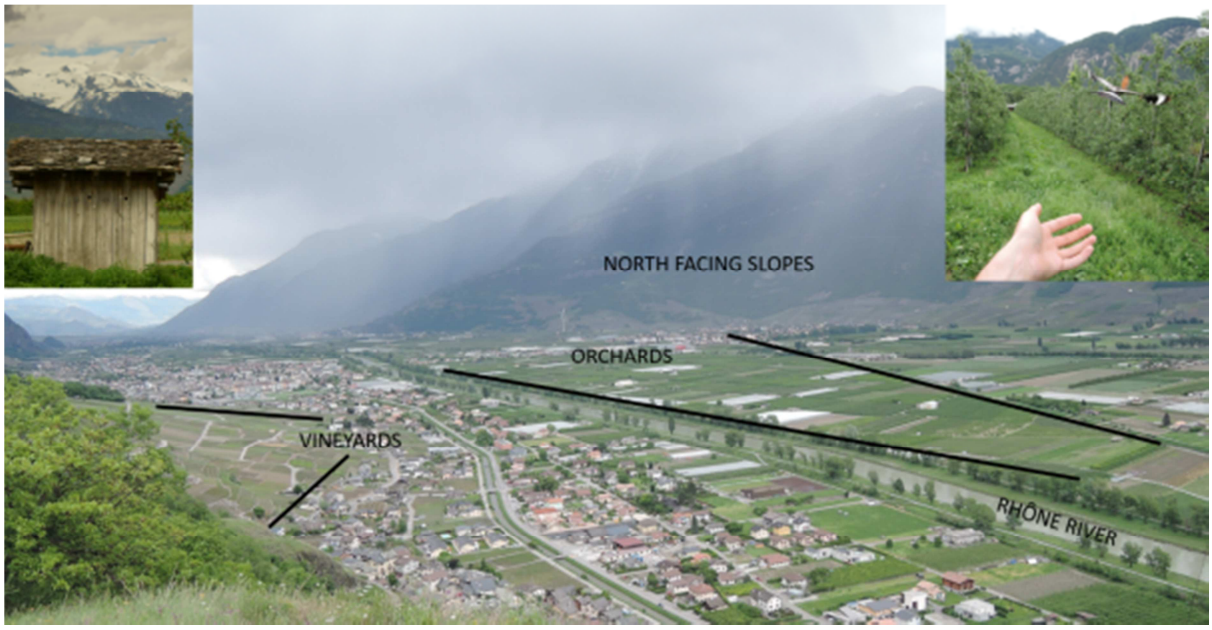

Figure 2. Cross section of the Rhône valley with the inset left showing a typical shed being used to install nestboxes in and the inset on the right showing the layout of an orchard.

Both species have been extensively studied over the past decade in the Rhône valley and studies have been published on Hoopoes on population dynamics (Arlettaz et al. 2010b, Schaub et al. 2012), breeding behaviour (Fournier and Arlettaz 2001, Bötsch et al. 2012, Hoffmann et al. 2015), foraging behaviour (Schaub et al. 2010, Tagmann-Ioset et al. 2012) and migratory behaviour (Reichlin et al. 2009, Bächler et al. 2010). Likewise on Wrynecks their population dynamics have been studied extensively (Ehrenbold et al. 2003, Ehrenbold and Schaub 2007, Coudrain et al. 2010, Schaub et al. 2012), as well as nesting site preferences (Zingg et al. 2010), feeding behaviour (Geiser et al. 2008), habitat preferences (Mermod et al. 2009, Weisshaupt et al. 2011) and migratory behaviour (Reichlin et al. 2009, 2010).

Thesis outline

Since most data was available on Hoopoes, these form the major part of the thesis. Chapter 2 focuses on the effects of geolocators on the physiology, survival and behaviour of Hoopoes; chapters 3 and 4 describe the migratory behaviour of Wrynecks using geolocators and observations in the wintering grounds; chapter 5 investigates the repeatability of migratory behaviour within individual Hoopoes; chapter 6 focuses on differences in timing in individual Hoopoes and their consequences on reproductive success and, finally; chapter 7 quantifies the effects of the previous breeding season and migration on current reproductive success.

A general problem when using any kind of device, is whether it might influence an individual's behaviour and thus potentially bias the results (Barron et al. 2010). Especially in migratory birds, the additional weight and drag might have a negative influence on the individual's fitness. It might influence their behaviour in such a way, that migration strategies are altered. **Chapter 2** describes whether Hoopoes that carried a geolocator for the course of one year, were negatively affected in their body condition, physiological state, breeding behaviour and annual apparent survival. No negative effects were found when data for all years were pooled, but some effects were found for individual years, however these were mostly positive for birds that had carried a geolocator. Hoopoes thus did not seem to be affected by the geolocator and thus birds that carried a geolocator can be considered representative for the population as a whole, also for the migratory behaviour they displayed.

Up to date, it has been assumed that Wrynecks from Central European populations, including the population we studied, are long-distance migrants that spend the winter in sub-Saharan Africa (Bauer et al. 2005). Using geolocator data, **Chapter 3** shows that in fact birds winter within the Iberian Peninsula and in Morocco. These findings have great implications for the conversation of Wrynecks throughout Europe, since they are likely under different selective pressure depending on their breeding origin and corresponding wintering areas. It was always assumed that the declines of Wrynecks were partly caused by habitat losses in sub-Saharan Africa, but causes clearly might have to be sought elsewhere.

Where exactly Wrynecks occur in winter and which habitat they prefer, is unclear to date. From the breeding grounds, it is apparent they prefer very specific half-open habitats with a high density of ants, which they mainly find in half open countryside, forests and orchards (Weisshaupt et al. 2011). **Chapter 4** describes the habitat preference of Wrynecks mid-winter in the Northern Extremadura, Spain. Given the geolocator results presented in the preceding chapter, it is not unlikely that some of these wintering Wrynecks belong to Central European populations. The fact that they occur in very specific habitats consisting of extensively used (irrigated) croplands, is of great importance for the proper conservation of Wrynecks throughout their annual cycle. This type of habitat is under pressure of disappearing as a cause of intensification of agricultural practices and thus further research and monitoring of Wrynecks and other wintering migrants on the Iberian Peninsula, is of great importance for adequate conservation measures.

It is most often assumed that migratory birds are very consistent in their migratory behaviour, since it would make them profit from previous knowledge on routes and wintering sites and since the timing of the annual cycle is constrained by different distinct life-history activities such as breeding and moult. Studies that investigated both the temporal and spatial repeatability of migration within the same system are however lacking to date. In **chapter 5** I study the individual repeatability of migratory behaviour in adult and first-time migrating Hoopoes. Interestingly, only the routes they follow in autumn were found to be repeatable, but all other aspects of migration were variable. This is contrary to current beliefs and forms a good example of the flexibility even short-lived birds as the Hoopoe can exhibit during the migratory phase of their annual cycle. Migratory birds might be much more capable of adapting to changing environmental conditions *en route* and in the wintering sites than thought to date, which would make them more resilient in coping with habitat and climate changes.

One of the most pressing questions in migration research, is whether consequences of a previous stage might carry-over to later stages (Harrison et al. 2011). Such dependencies could control the annual cycle of a migratory bird whereby an individual that starts migration late, will be late throughout and subsequently will arrive late at the breeding grounds, which is assumed to negatively affect its breeding success. Potential for compensation to counter-act 'mistiming' is presumably low, especially during timing of events closer towards arrival back in the breeding grounds. **Chapter 6** investigates the timing of breeding and migration, the dependencies between successive events, variability of the timing of these events, potential for compensation and finally the effect of timing on reproductive success. It was found that the timing of proceeding events were highly correlated throughout migration. Variability of the timing of events decreased towards arrival back in the breeding grounds. The wintering period, but also in part the post-breeding, autumn and spring migration period seemed to have potential for compensation of delays build up previously. Arrival in the breeding grounds however was more related to the duration of the spring migration journey, rather than solely the departure date from the wintering grounds. Furthermore, we could show that indeed a later arrival led to later onset of breeding and fewer fledglings. There is thus a fitness consequence of migration timing, but it occurs only in the final stage before breeding.

Disentangling and quantifying the effect of different migratory stages on the current breeding success, is a difficult task, since these stages depend on each other to different degrees as explored in chapter 6. **Chapter 7** describes the use of a structural equation modelling approach to quantify the effects of both previous breeding success and individual migration strategies on current breeding success. Effects of timing decisions were found to dilute with progressing migration and for the current breeding success mainly the previous breeding success seemed of importance. Rather than the migratory behaviour in itself, it thus seems that individuals with a higher intrinsic value, i.e. higher previous breeding success, are more likely to have a higher breeding success the subsequent year, regardless of their actual migratory procession.

CHAPTER 2 – NO DETECTABLE EFFECTS OF LIGHTWEIGHT GEOLOCATORS ON A PALAEARCTIC-AFRICAN LONG-DISTANCE MIGRANT

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Abstract

Tracking devices are used in a broad range of species for a broad range of questions, but their potential effects on study species are debated. Outcomes of earlier studies on effects are equivocal: some studies find negative effects on behaviour and life history traits, while others do not. Contrasting results might be due to low sample sizes, temporal scale (no repetition of the study over multiple years) and a limited range of response variables considered. We investigated effects of geolocators on a range of response variables: body condition, physiological states, reproductive performance and, ultimately, annual apparent survival for a medium-sized Palaearctic-African long-distance migrant, the Eurasian Hoopoe *Upupa epops*, for the combined study period (2009–2014) and for individual years. We investigated response variables 1 year after deployment of the geolocator and found no differences in body condition, physiological states and several components of reproductive performance between individuals with and without geolocators when data were combined. Also, apparent annual survival did not differ between geolocator and control birds. We did, however, find effects in some years possibly related to environmental stochasticity or chance events due to lower sample sizes. We argue that results of studies on the effects of tracking devices should be interpreted and generalized with great caution and suggest that future studies on the effects of tracking devices are conducted over multiple years. Future studies should also apply capture–recapture models to estimate survival, rather than focus solely on return rates.

Keywords: Body condition, Capture–recapture model, Corticosterone, Migration, Survival, Hoopoe

Introduction

Following individual animals through time and across space usually requires the use of tracking devices, which either actively transmit or archive data, e.g., radio transmitters, geolocators (light archiving loggers) or GPS loggers (Bridge et al. 2011). Despite miniaturization of such devices over the last decades, tracking devices can affect the condition and behaviour of individuals carrying them and, ultimately, their fitness. The additional weight and drag may increase energy expenditure (Bowlin et al. 2010, Vandenabeele et al. 2012, Pennycuick et al. 2012), while friction of the device can cause injuries (Rodríguez et al. 2009, Peniche et al. 2011).

Even though it is commonly acknowledged that effects can occur, evidence is equivocal for many investigated traits such as body condition (Adams et al. 2009, Barron et al. 2010), physiological state (Barron et al. 2010, Quillfeldt et al. 2012), components of reproductive performance like onset of breeding (Quillfeldt et al. 2012, Arlt et al. 2013) or fledgling mass (Ackerman et al. 2004, Quillfeldt et al. 2012), and also survival, usually investigated in the form of return rates (Phillips et al. 2003, Rodríguez et al. 2009, Barron et al. 2010, Townsend et al. 2012, Costantini and Møller 2013, Arlt et al. 2013, Scandolara et al. 2014, Gómez et al. 2014). Because these traits may be differently affected by the tracking device, it is difficult to draw general conclusions on device effects when only one or a few traits are studied. For instance, when solely reporting the effects on return rates or onset of the reproductive season, one might well miss the effects on other fitness-related traits such as stress levels. Different tracking devices might cause different effects due to their divergent type of attachment (leg-loop harness, wing-loop harness, elastic versus rigid loops, fixed to bands, glued to feathers), shape (with antenna, light stalk, without any appendices) and duration of deployment (few hours up to several years).

Negative effects of tracking devices might be particularly apparent in migrating animals carrying a device for at least 1 year. Migrants face multiple challenging phases during their annual cycle, during which optimal energy management is crucial for successful reproduction and to survive. A tracking device that is increasingly being used is a lightweight geolocator. These register light intensity by which positions can be estimated and are usually carried for approximately 1 year. A meta-analysis on the effects of geolocators on birds showed survival to be negatively affected for tagged birds (Costantini and Møller 2013). However, the effects could be statistically supported only when combining all data; most individual studies had insufficient sample sizes to draw conclusive results. Furthermore, none of these studies considered more than three seasons, although the magnitude of effects may vary from year to year due to environmental variation (Pietz et al. 1993, Bro et al. 1999, Hupp et al. 2006).

The equivocal effects of geolocators can result from many reasons, such as size and mode of attachment of the device, behaviour of the study species and the weight of the devices relative to the weight of the study species. Moreover, equivocal effects might result from low sample sizes, the temporal scale of the study (no repetition over multiple years) and a restrictive range of the studied traits. To date, a comprehensive study on the effects of carrying a geolocator over an entire year on a wide range of traits over multiple years is still lacking.

To fill this gap, we aimed to identify the effects of geolocators on several life-history traits of a Palaearctic-African migratory bird, the Eurasian Hoopoe (Upupa epops), over a 7-year period. We compared body condition, physiological states, several components of reproductive performance and survival between geolocator and control birds. We investigated whether the effects were present over the whole study period combined and for each year separately.

Material and Methods

Study population and data acquisition

We studied geolocator effects in a population of Hoopoes breeding in nestboxes in the Valais, south-western Switzerland (46_140N, 7_220E). The study area is about 62 km2 in area and harbours ~550 nestboxes (Arlettaz et al. 2010a). Hoopoes feed on large soil invertebrates and birds from this population are long-distance Palaearctic-African migrants, which spend the non-breeding season in the Sahelian belt south of the Sahara (Bächler et al. 2010). They typically return to the breeding grounds from the beginning of April, start breeding in late April and the last nestlings fledge in early August. Most Hoopoes in our study population produce only one clutch a year, but about one-third have two or more clutches (Hoffmann et al. 2015). Birds were caught in or at the nestboxes which were checked every 10–14 days from mid-April until mid-July each year.

To investigate geolocator effects, we studied several traits both for the whole study period combined as well as for each individual year. We investigated traits that might indicate short-term effects [body condition, physiological states (baseline corticosterone, stress response), components of reproductive performance (territory occupancy, onset of breeding, brood success, number of fledglings, fledgling weight, average food biomass delivered to the nest per hour and per visit] of carrying a geolocator, and survival as an indication of a long-term effect. For a definition of each response variable, see Table 2B (below).

Data collection

Between 2008 and 2013, 328 breeding birds were equipped with geolocators of type SOI-GDL1 (Bächler et al. 2010) of which 81 were recaptured between 2009 and 2014. These geolocators have a light stalk of 10 mm positioned under an angle of 45° on the geolocator and weigh on average 1.32 g including a leg-loop harness, which corresponds to ~1.9 % of the body mass of a Hoopoe. As a control group for birds that were recaptured with a geolocator after 1 year, we used 273 individuals that never carried a geolocator (see Table 1 for the annual sample size).

Birds were caught at least 5 days after their young had hatched and were given a unique combination of a metal ring and three colour rings. Following this procedure, about 85–90 % of our study population was marked and measured each year. We only used data of the first capture or of the first time a bird was equipped with a geolocator; we excluded repeated tracks in all analyses except the capture–recapture analysis. We did this to exclude the possibility that birds compensate their behaviour or physiology for carrying a geolocator over longer deployments, which would lead to an unfair comparison. To obtain a measure of body condition, we recorded mass to the nearest 0.1 g and measured maximum chord wing length to the nearest 0.1 mm, and calculated their ratio. Data were obtained between 2009 and 2014.

Table 1. Number of Eurasian Hoopoes(*Upupa epops*) with (*Geolocator*) and without (*Control*) a geolocator used in the different models on body condition, physiological states and components of reproductive performance for each year, more details see text.

Year	**# returning birds measured**		**# returning birds measured with brood success**		**# birds sampled for corticosterone**	
	Control	Geolocator	Control	Geolocator	Control	Geolocator
2009	54	14	50	13		
2010	56	14	51	13	28	7
2011	61	10	55	9	30	9
2012	28	12	26	9	43	9
2013	27	12	21	9	16	22
2014	47	19	44	16		
Total	**273**	**81**	**247**	**69**	**117**	**47**

Corticosterone as a measure of physiological state was sampled during the reproductive seasons 2010–2013 by taking blood from 164 breeding birds (117 control and 47 equipped birds; Table 1) when they were feeding their nestlings. We obtained measurements of baseline and stress response following the method described in Schmid et al. (2013): all included baseline samples were taken within 3 min after capture; which is within the time limit after which baseline corticosterone might be affected (Romero and Reed 2005). Only individuals for which we had data for both corticosterone levels were included.

To investigate the different components of reproductive performance, occupied nestboxes were visited every 3 days to obtain accurate data on numbers of eggs, hatchlings and fledglings, and on breeding phenology. Nestlings were ringed at an age of c.18 days and were weighed to the nearest 0.1 g. All these data were available for the reproductive seasons 2009–2014.

Data on parental care in terms of delivered prey biomass were collected in just 1 year (2012) for 45 pairs. We analysed prey biomass delivered per hour and per visit when nestlings were about 2 weeks old. These data were acquired using video recordings with estimated weights for each prey size/species (for more details, see Guillod 2013).

Analysis of body condition, physiological states and reproductive performance

Explanatory variables are listed in Table 2a and definitions of response variables in Table 2b. Additionally, models on body condition and physiological states included breeding phase: the time between onset of breeding and capture. The model on physiological states furthermore included age, capture time, the time between capture and the first blood sample when baseline corticosterone was measured (delta 1, minimum 0.33, mean 1.45 and maximum 4 min), and the time between capture and the second blood sample when the stress response was analysed (in minutes, delta 2; see Table 2 for a complete description of variables used). The model on parental care (Table 2A) additionally included the age of nestlings, frequency of visits, and territory (as a random factor) as explanatory variables.

To test for geolocator effects we used generalized linear mixed effect models with year as a random effect to study effects over the whole study period and generalized linear models to investigate each year separately. The analyses were conducted with R 3.1.0 (R Core Team, Vienna, 2014) using the function lmer and glm. The best model for each dependent variable was selected using a step-wise backwards procedure with the package lmerTest (Kuznetsova et al. 2015). To illustrate each model's results, we made posterior predictions for geolocator and control individuals using parametric bootstrapping of 1000 simulations with the package *arm*.

Table 2. Definition of the maximal models for all traits (A) and the definition of the used explanatory variables (B). The year effect and territory were always random, all other explanatory variables were fixed. The models per year were the same, but they contained no year effect. For more details, see text.

A

Description	Response	Explanatory variables									
body condition	condition	geolocator	-	sex	-	onset breeding	occupancy	breeding phase	-	-	year
physiology	baseline cort	geolocator	age	sex	condition	onset breeding	occupancy	breeding phase	delta 1	capture time	year
	stress response	geolocator	age	sex	condition	onset breeding	occupancy	breeding phase	delta 2	capture time	year
components of reproductive performance	occupancy	geolocator	-	sex	condition	onset breeding	-	-	-	-	year
	onset breeding	geolocator	-	sex	condition	-	occupancy	-	-	-	year
	brood success	geolocator	-	sex	condition	onset breeding	occupancy	-	-	-	year
	# fledglings	geolocator	-	sex	condition	onset breeding	occupancy	-	-	-	year
	weight fledgling	geolocator	-	sex	condition	onset breeding	occupancy	-	-	-	year
parental care	biomass^{-hour}	geolocator	age	sex	condition	onset breeding	occupancy	age nestlings	-	territory	-
	biomass^{-visit}	geolocator	age	sex	condition	onset breeding	occupancy	age nestlings	frequency	territory	-

B

Model variable	Description
age	either second year or after second year
wing length	maximal chord: the distance on the closed wing from the foremost extremity of the carpus to the tip of the longest primary feather (in mm, Svensson 1992)
territory occupancy	the number of years the nestbox was occupied divided by the total number of years it was installed as of 2002 (indication of territory quality, Tschumi, Schaub, & Arlettaz, 2014)
onset of breeding	date of first egg laying in Julian day, calculated backwards from the number of eggs upon the first visit (sequential laying of one egg per day)
breeding phase	time between onset of breeding and capture (in days)
body condition	body weight (g) divided by wing length (mm)
delta 1	time between capture and taking the first blood sample (in minutes)
capture time	time of the day the bird was captured as a fraction of 24 hours (e.g. 0.50 is noon, 12:00)
delta 2	time between capture and the second blood sample (in minutes, minimum 20)
brood success	successful when at last 1 nestling fledged, for a given year only the very first brood attempt was considered
# fledglings	number of fledglings (nestlings that left the nestbox after ~28 days after hatching) in successful first broods
weight fledgling	average weight (g) of nestlings at time of ringing (age ~18 days) that fledged
biomass / hour	average biomass (g) of prey items delivered per hour per bird
age nestlings	age of the nestlings at the time of filming (~2 weeks)
biomass / visit	average biomass (g) of prey items delivered per visit

Recapture probabilities and annual survival

We used a capture–recapture model to estimate survival, taking into account detection probability and the potential loss of a geolocator. We used a multi-event model framework (Pradel 2009), which links field observations to biological states of individuals. We defined the following states: ''Alive with geolocator'' (G+), ''Alive without geolocator'' (G-) and ''Dead'' (D). However, we handled birds at recapture and equipped some of them with a geolocator, thereby modifying their states in a deterministic way. To account for this, we added a dummy capture occasion after the real capture occasion and therefore expanded the biological states with ''Alive and equipped with geolocator'' (S), ''Alive and not equipped'' (R), ''Alive with geolocator but outside the study population'' (AE-) and ''Alive without geolocator but outside the study population'' (AE-). At each capture, birds could be in states G-, G- or D. At the following dummy occasion (*t'* + *1*), captured birds were assigned state S or R, while non-captured birds were assigned state AE? or AE- (see Appendix A for a complete description of the model). This model allowed us to estimate loss rate (*L*) and survival probability (φ) while accounting for imperfect detection (*ρ*) of birds and deterministic changes of individual states.

We investigated effects of year, sex and geolocator on survival and recapture probabilities, and effects of year and sex on geolocator loss probability: L_{y*sex}, Φ_{y*sex}, $P_{sex*geo}$ with *y*, *sex*, and *geo* the effects of year, sex and geolocator, respectively.

To investigate whether the structure of the model was appropriate and included major sources of heterogeneity, we performed a goodness-of-fit of the capture–recapture model using the program U-CARE (Choquet et al. 2009b). The model selection followed a step-down approach (Lebreton et al. 1992), starting with the initial model and sequentially fitting models with constrained parameterization for detection, loss and survival probabilities. Model selection relied on Akaike's information criterion (Burnham and Anderson 2002). Model selection and parameter estimations were performed using the program E-SURGE (Choquet et al. 2009a).

Results

Body condition, physiological states and components of reproductive performance

Neither body condition, physiological states nor any component of reproductive performance were affected by carrying a geolocator when data of all years were pooled (Fig. 1; Appendix B, Tables S1–S3). When geolocator was added to the final model, effect sizes were very small (Table S4).

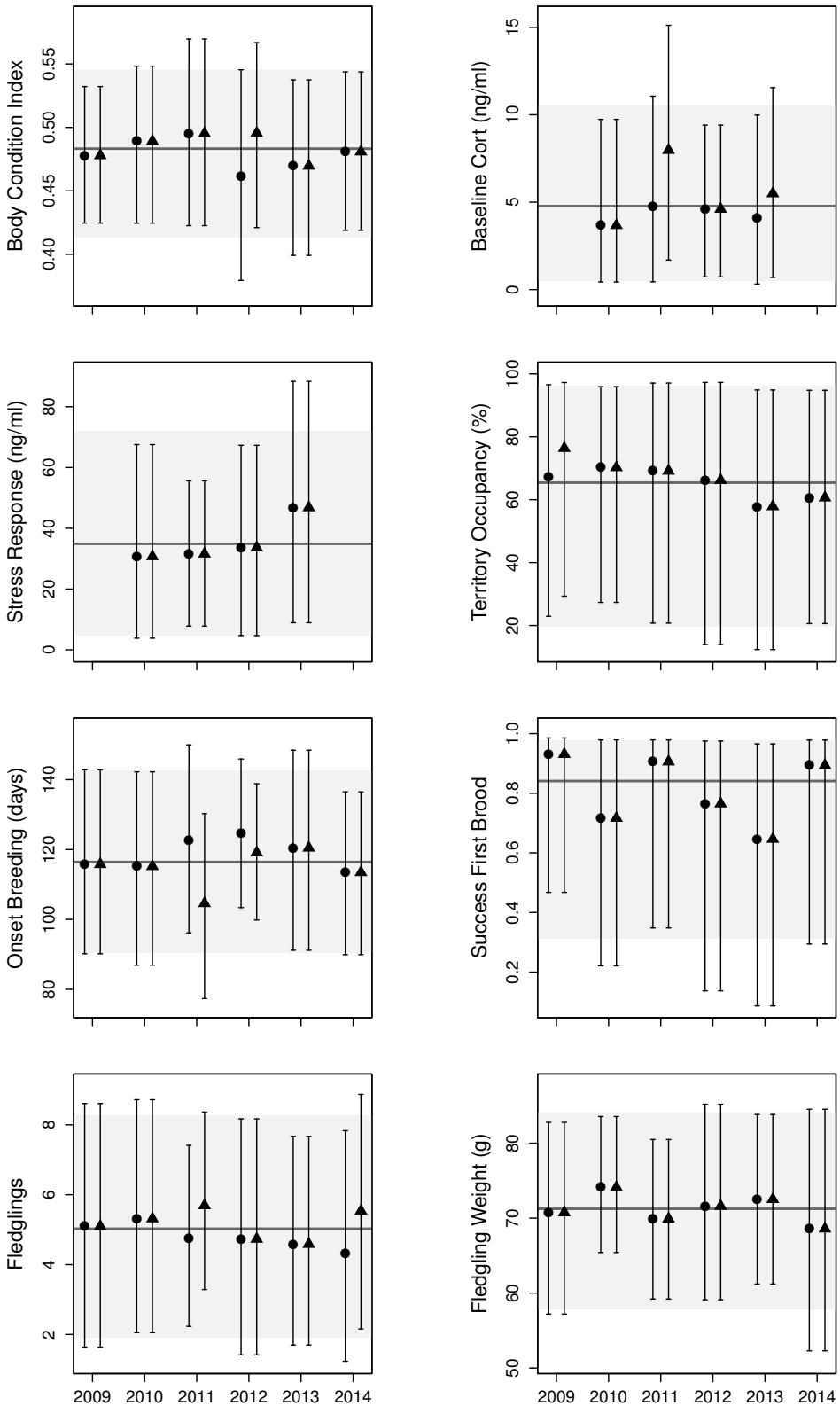

Figure 1. Summary of model predictions using 1000 simulations for response variables studied over multiple years. *Points* represent control and *triangles* geolocator Eurasian Hoopoes (*Upupa epops*), respectively. Median and 95 % spread of the data are indicated. The *line* indicates the median for all years combined, the *gray area* the 95 % distribution. For more information, see text and Appendix B, Tables S1 – S3; for estimated sizes of geolocator effects, see Appendix B Table S5.

We found differences in several traits between geolocator and control birds in individual study years, but, contrary to our expectations, these were mostly positive for geolocator birds (Fig. 1): (1) their body condition was higher in 2012 (Table S1); (2) they tended to occupy better territories in 2009 (Table S3 A); (3) their onset of breeding was earlier in 2011 (~2 weeks) and in 2012 (~5 days) (Table S3 B); and (4) the number of fledglings of successful first broods was higher in 2011 and 2014 (~1 more fledgling; Table S3 D). We only found negative effects for baseline corticosterone, which was slightly elevated for geolocator birds in 2012 (Table S2 A).

Annual survival and recapture probabilities

The goodness-of-fit test of the capture–recapture model was not significant (χ^2 = 18.78, *df* = 26, P = 0.85) indicating an appropriate structure of our initial model.

Based on AIC, the most supported model included sex, a temporal trend in survival and constant parameters for loss and detection probabilities (model 15, Table 3), but a geolocator effect was not retained. The best model including a geolocator effect on apparent survival was considerably worse (model 10, Table 3).

The recapture probability was very high (0.88 ± SE 0.04), suggesting most marked birds were detected and captured each year. The annual loss rate was high with about one-quarter of geolocators lost (0.28 ± SE 0.04).

The mean annual apparent survival probability over the whole study period was 0.35 ± 0.02 (from model 13, best model without time variation). Survival of geolocator individuals was lower compared to survival of control individuals (0.33 ± 0.04 vs. 0.36 ± 0.02, from model 10), but confidence intervals of both estimates overlapped for all years (0.27–0.41 vs. 0.31–0.41; Fig. 2).

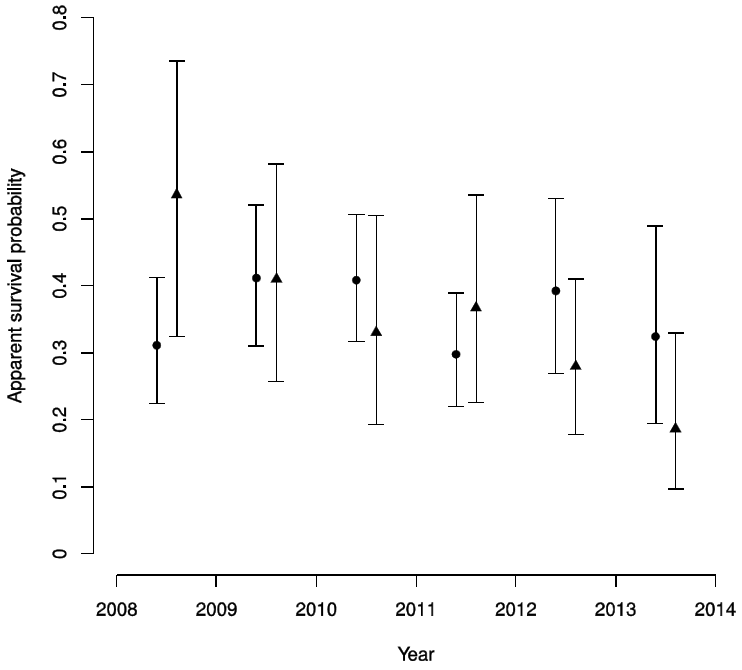

Figure 2. Point estimates and 95 % confidence intervals (from Model 7) of survival probabilities of Hoopoes with (*points*) and without geolocator (*triangles*)

Table 3. Model selection results for the effects of year, sex and geolocator on loss, survival and detection probabilities of Hoopoes ringed from 2008 to 2013 and reencountered from 2009 to 2014. For each model, we give the number of estimated parameters (*K*), the deviance, difference in Akaike's information criterion (*ΔAIC*) and Akaike weight (ω).

Model	Loss rate	Survival	Recapture	K	Deviance	ΔAIC	ω
15	*i*	*sex*T2*	*i*	7	2391.24	0.0	0.86
14	*i*	*T*	*i*	4	2402.03	4.8	0.08
13	*i*	*i*	*i*	3	2406.71	7.5	0.02
12	*i*	*sex*	*i*	4	2405.14	7.9	0.02
10	*i*	*geo*	*i*	4	2406.45	9.2	0.01
11	*i*	*y*	*i*	8	2399.28	10.0	0.01
8	*i*	*sex*geo*	*i*	6	2404.53	11.3	0.00
9	*i*	*y*sex*	*i*	14	2388.88	11.6	0.00
7	*i*	*y*geo*	*i*	14	2390.89	13.6	0.00
6	*i*	*y*geo*sex*	*i*	26	2372.01	18.8	0.00
5	*y*	*y*geo*sex*	*i*	31	2363.91	20.7	0.00
4	*sex*	*y*geo*sex*	*i*	27	2371.99	20.8	0.00
3	*y*sex*	*y*geo*sex*	*i*	37	2362.78	31.5	0.00
2	*y*sex*	*y*geo*sex*	*geo*	38	2362.03	32.8	0.00
1	*y*sex*	*y*geo*sex*	*geo*sex*	40	2358.33	33.1	0.00

Model notation: *sex*: sex effect, *geo*: geolocator effect, *y*: year effect, *T*: linear time effect, *T2*: linear year effect but we excluded the first year for males only, *i*: intercept, "*" interaction.

Discussion

We found no effect of geolocators on any of the investigated traits when data of all years were pooled: body condition, physiological state, reproductive performance and survival did not differ between geolocator and control birds. This is in contrast to many earlier studies (mentioned in Costantini and Møller 2013), yet most of those focussed solely on the effects of a few traits that were assessed during just 1 year with relatively low sample sizes. When we analysed data for each year separately, some traits did differ between geolocator and control birds.

Effects of geolocator on life-history traits for the combined study period

A prominent reason why the geolocators had essentially no effect on different traits of Hoopoes could be the relative low weight of the devices we used (~2 % of body mass). However, it has been shown that even for weights below 2 %, the effects of a device might be profound in some species. For example, the effects are more pronounced in seabirds where devices would have to be streamlined both in the air as well as underwater (Vandenabeele et al. 2012). Moreover, aerial foragers were especially negatively affected by carrying a geolocator which might relate to the extra drag of the device (Costantini and Møller 2013). Hoopoes are landbirds that mainly forage on larger soil invertebrates and thus might be less affected by carrying a device. Lastly, Hoopoes are not known to make long, nonstop flights, but rather have multiple stopovers along the way (Bächler et al. 2010).

The glucocorticoid hormone corticosterone orchestrates many physiological processes, including energy mobilization (Bonier et al. 2011) and reproduction (Schmid et al. 2013), and it also affects behaviour (Coppens et al. 2010). The physiological role of corticosterone is quite distinct depending on whether it circulates at low baseline or at high acute stress-induced levels. At low baseline levels, corticosterone is involved in maintaining physiological homeostasis in everyday life (Romero 2004). In response to stressful events, however, corticosterone is released in high amounts into the blood and helps to mobilize energy and to redirect the behaviour to self-maintenance (Sapolsky et al. 2000). While a short-term release of corticosterone is considered beneficial in allowing individuals to overcome threatening situation, chronically elevated levels can entail negative long-term effects (Sapolsky et al. 2000). If geolocators were to evoke stress in the Hoopoes, for instance by the higher weight they have to carry or by hampering their flight performance, we would expect an increased level of circulating baseline corticosterone and/or a reduced release of corticosterone in response to handling. However, we found no effects on baseline corticosterone and stress response. This might be related to the low relative weight of the geolocators (<2 % of the body weight) or because, over the course of 1 year, the birds got used to the geolocator and thus stress levels returned to normal. Other studies, however, have shown increases in both baseline corticosterone and stress response after 1 year of deployment (Elliott et al. 2012, Quillfeldt et al. 2012), though a very recent study that investigated corticosterone in feathers for two aerial feeding migrants also did not find any differences (Fairhurst et al. 2015).

Even though their condition and physiological states might be the same, there could still be differences in reproductive performance, but we found no effects of geolocator on any component of reproductive performance, not even on finer-scale traits such as fledgling mass and food provisioning rates, contrasting with the majority of the literature (Ackerman et al. 2004, Adams et al.

2009, Barron et al. 2010, Costantini and Møller 2013). For example, we found no difference in the onset of breeding, an important trait that is directly linked to the quality of the territory occupied and thus indirectly to reproductive success: birds that arrive later in the breeding grounds are forced to occupy lower quality territories and therefore would have a lower reproductive success (Tschumi et al. 2014).

Survival was often found to be negatively affected for geolocator birds (Costantini and Møller 2013). In almost all studies, the effect of geolocators on survival was assessed based on return rates. However, return rates are the product of the probabilities to survive and to be recaptured. Consequently, return rates can only be used as an index of survival, if recapture probabilities for individuals with a geolocator and for control individuals are identical. Since researchers often target catching birds with geolocators to retrieve the data, resighting and thus recapture probabilities of geolocator birds are likely to be elevated. Moreover, if a study is restricted to breeding individuals, recapture probability is affected by the probability to breed, which itself might be affected by the geolocator. Consequently, return rates cannot be used to evaluate the effects of geolocators on survival, because they depend on strong assumptions that remain untested. Using a capture–recapture framework, we found no difference in recapture probability between geolocator and control birds for our study population, suggesting an equal effort to detect both groups of individuals. Furthermore, the high recapture rate in our study, due to a systematic search for birds in the study area, allowed us to accurately estimate demographic parameters. By also taking into account geolocator loss, we are thus confident in our estimates of survival and our finding that carrying a geolocator did not induce a negative effect on annual survival.

Interannual variation in geolocator effects

Although we found no differences between geolocator and control birds for the combined study period, some traits differed in specific years. These differences can most likely be explained by low sample sizes in some years, most particularly in 2012 when we only had 5 control versus 12 geolocator individuals, and for which we found geolocator birds to be in better body condition and to start breeding earlier. In later years, smaller numbers of control individuals were available, because the largest part of the population were equipped with a geolocator. Therefore, the pool of control birds that never had a geolocator got smaller.

Another explanation for the differences could also be related to interannual variations in environmental conditions, be it on the nonbreeding grounds, along the migration route or upon arrival back in the breeding grounds. For instance, body condition of Montserat Orioles (Icterus oberi) was lower when pre-breeding rainfall was low (Oppel et al. 2013) and reproductive success in shrubsteppe sparrows was greater in years with wetter compared to drier conditions in the breeding

grounds (Rotenberry and Wiens 1991). Carrying a device might be an additional constraint in such years with harsher conditions (Pietz et al. 1993, Bro et al. 1999) affecting traits negatively, while under 'normal' environmental circumstances a device might exhibit no effect.

Conclusion

It is clear that tracking devices allow sampling very valuable data for fundamental and conservation-oriented research, but results should be interpreted with caution. Besides animal welfare issues, inference based on such data can be compromised if the tracking device affects the behaviour or performance of the individuals or because they induce a selection towards strong individuals. Here, we found no effect of geolocators for a European population of medium-sized near-passerine birds, the Eurasian Hoopoe. Even though effects of devices are likely linked to the relative weight of the device and the individual's behaviour and are thus species-specific, such results could be similar for other medium-sized ground-foraging migrants, such as Rollers (*Coracias garrulus*) or birds where the geolocators have a similar relative weight (<2 %).

Furthermore, our study shows that results can only be considered robust when looking at several years and at a range of life-history traits. We thus recommend investigating effects of tracking devices over several years to include a range of particular environmental conditions and to focus on a broad array of variables. Finally, using a capture–recapture model as proposed here may be a better way to investigate demographic parameters than solely reporting return rates.

Acknowledgments

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CHAPTER 3 – SHORT-DISTANCE MIGRATION OF WRYNECKS JYNX TORQUILLA FROM CENTRAL EUROPEAN POPULATIONS

Rien E. van Wijk, Michael Schaub, Dirk Tolkmitt, Detlef Becker & Steffen Hahn

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Abstract

To date, European Wrynecks *Jynx torquilla torquilla* have been considered to be long distance Palaearctic-African migrants that spend the non-breeding season in Sahelian Africa, where they have been reported regularly. Results from tracking individual birds showed that Wrynecks from two central European populations migrated only relatively short distances (*c*. 1500km and 3000km) to the Iberian Peninsula and North-western Africa, compared to a minimum distance of about 4500km to Sahelian Africa. Additionally, differences in wing lengths of populations from central and northern Europe support the idea of leap frog migration, populations from northern Europe being long-distance migrants with a non-breeding distribution in Sahelian Africa.

Keywords: geolocator, long-distance migration, non-breeding, sub-Saharan Africa, tracking, wing length, woodpecker.

Introduction

Eurasian Wrynecks *Jynx torquilla* show a large variation in migratory behaviour at the subspecies level. *J. t. tschusii* breeding on the Apennine Peninsula and the eastern Adriatic coast, and *J. t. mauretanica* from the Balearic Islands and northern Africa, are resident, as are southern European populations of the nominate *J. t. torquilla* (Cramp *et al.* 1985, Zwarts *et al.* 2009). All other populations of the nominate form are supposed to migrate to Sahelian Africa; populations from N/NW Europe migrate via the British Isles and the Iberian Peninsula and populations from NE/Central Europe migrate via the Apennine and Balkan Peninsula (e.g. Cramp *et al.* 1985, Zwarts *et al.* 2009). Eastern Eurasian populations probably migrate via the Arabian Peninsula to Africa or further east to southern Asia (Priklonskii *et al.* 2005). This is also reflected in morphological features: the resident subspecies *Jynx t. mauretanica* has a wing length of around 79mm, *Jynx t. tschusii* around 84mm and the migratory nominate form *Jynx t. torquilla* has a wing length of about 89mm (e.g. Eck & Geidel 1973, Brichetti & Fracasso 2007). Additionally, Eck and Geidel (1973) showed that Wrynecks of the nominate form from Northern Europe and Central Europe have the most pointed, longest wings with a relatively short tail, while birds of the subspecies *Jynx t. tschusii* and *mauretanica* from around the Mediterranean Sea have both short wings and short tails.

The non-breeding areas, i.e. the main areas of residency during the non-breeding period, are thought to include the entire Sahelian savannah belt from Senegal in the west to northern Kenya in the east (e.g. Cramp *et al.* 1985), based mainly on direct observations of Wrynecks at various places. However, only a few ring recoveries from Africa exist: two Wrynecks from Sweden and one individual from Spain have been recovered in Morocco, and one individual from the Czech Republic has been recovered in Libya, suggesting population-specific passage areas and/or non-breeding areas (Reichlin *et al.* 2009, SEO/Birdlife 2012).

There is also indirect evidence for the location of the Wrynecks' non-breeding areas in Sahelian Africa in that changes in population index of several European breeding populations (including populations from Germany) were negatively correlated with a precipitation index of the western Sahel (Zwarts *et al.* 2009). Additionally, stable isotope analysis of feathers grown during the boreal winter predicted a non-breeding area in the western Sahel zone and western Sudan/Ethiopia for a German population of Wrynecks, and non-breeding areas that include almost the whole of sub-Saharan Africa and, with lower probability, southern parts of the Iberian Peninsula and north-western Africa (Reichlin *et al.* 2010), for a Swiss population. Despite many observations of Wrynecks of unknown origin in Africa (Cramp *et al.* 1985), population-specific wintering ranges are still

unknown. In this study, we determined the non-breeding areas of Wrynecks from two Central European populations in Germany and Switzerland using geolocators.

Methods

The study population in south-western Switzerland (46°14'N 7°22'E) breeds in an intensive agricultural landscape with fruit tree plantations and vineyards. The study population in eastern Germany (52°01'N 13°04'E) is located in a former military training area, now covered by arid and semiarid grassland and managed grassland with fruit trees. Both populations breed in nest boxes. Wrynecks from both populations belonged to the nominate subspecies *Jynx t. torquilla*.

During the breeding season of 2011 (May till July), we randomly captured 43 adult breeding Wrynecks in Switzerland and 10 in Germany, either in the nest box or at the nest box entrance, and then fitted these birds with geolocators. We did not determine sex in the field since Wrynecks are monomorphic and cloacal protuberance did not allow sex discrimination. To compare recapture rates in 2012, we used adult breeding birds, which were ringed only as a control group. Geolocators (SOI-GDL1.0 incl. 5mm long light guide stalk Swiss Ornithological Institute) were mounted on the birds' back using a leg-loop silicon harness. The device including harness weighed 1.2 *g*, corresponding to 3.0-4.0% of adult body-weight (average body-weight 36.3 *g*, range 30-45 *g*, *n* = 198 Wrynecks caught in both study sites in 2011 and 2012).

Data analysis

We used the threshold method for positioning by light (Hill 1994, Lisovski *et al.* 2012). Sunrise and sunset times were determined using GeoLocator software (Swiss Ornithological Institute unpubl.). Non-natural sunrises/-sets, e.g. when entering a nestbox/cavity before sunset and leaving after sunrise, were removed for the calculation of geographic position. We determined non-breeding stationary periods by the ChangeLight function (R package GeoLight 1.02, probability of change = 0.8, minimum stationary period = 3 days; Lisovski & Hahn 2012). Having defined stationary periods, data for individual non-breeding areas were calibrated using Hill-Ekstrom calibration by minimising the variance of latitudes using a range of sun elevation angles (see Lisovski *et al*. 2012). The site-specific sun elevation angles varied between -3.8° and -6° (mean = -5.2°). We then filtered all outlying positions with distances > 800km from the median latitude of the respective non-breeding area. For the filtered positions, we applied kernel density estimation using ArcMap 10.0 (ESRI) with a search radius of 200 km. We calculated kernel densities encompassing 80% and 90% of the maximum density.

Wing length

We gathered data on wing length of nominate Wrynecks from different European breeding sites and on migration. Besides our study sites, we acquired data on breeding populations in Norway (Revtangen Ornitologiske Stasjon, T. Lislevand, pers.com.) and from two passage sites, Col de Bretolet, Switzerland and Ouadâne, Mauretania (Swiss Ornithological Institute, unpubl. data). Data from the Swiss breeding birds consisted only of length of the third primary (P3). We therefore recalculated wing length using a linear regression of wing length against P3 from birds caught in April 2013 in Switzerland using tape-luring (wing length (mm) = 0.876 ± 0.066 (SE) × P3 length (mm) + 30.49 ± 4.27 (SE), R^2 = 0.71, n = 76).

Results

Seven Wrynecks from the Swiss population equipped with geolocators were recaptured in 2012 (16.3%). One bird had lost the device. In controls, recapture rate was 11.8% (mean annual local return rate in period 2002-2009 = 16.1%, range 7.3-32%). For the German population, one individual with a geolocator was recaptured in 2012 (10%). In controls, recapture rate was 16.7% (mean annual local return rate in period 2009-2011 = 20.7%, range 12-27.6%; mean 2002-2008 = 15.7%). The body mass of Wrynecks returning with a geolocator was not significantly different from the control group (median of 37 *g* in controls and 36 *g* for birds with a geolocator, Mann-Whitney Rank Sum Test, control group 2012 n = 102, P = 0.11).

We found that birds from Switzerland used non-breeding areas in Portugal (n = 2), Spain (n = 3) and Morocco (n = 1): the single individual from Germany spent the boreal winter in Morocco (Figure 1A); no bird in our study spent the non-breeding season in Sahelian Africa. The loxodromic distance between the centroid points of breeding and non-breeding areas for the Swiss birds ranged from 1250-1950km, averaging 1500km, whereas the German Wryneck covered 3050km (Figure 1B).

One Wryneck from the Swiss population arrived in the non-breeding area on 6 September, and all others between 2 and 16 October (on average 3 October, supplementary material). The Swiss birds subsequently stayed in their non-breeding areas for 141-186 days (Figure 1C, on average 157 days), and departed from the non-breeding areas between 2 and 9 March (on average 6 March). The Wryneck from the German population arrived in the non-breeding area on 2 October, stayed there for 166 days, and departed on 15 March.

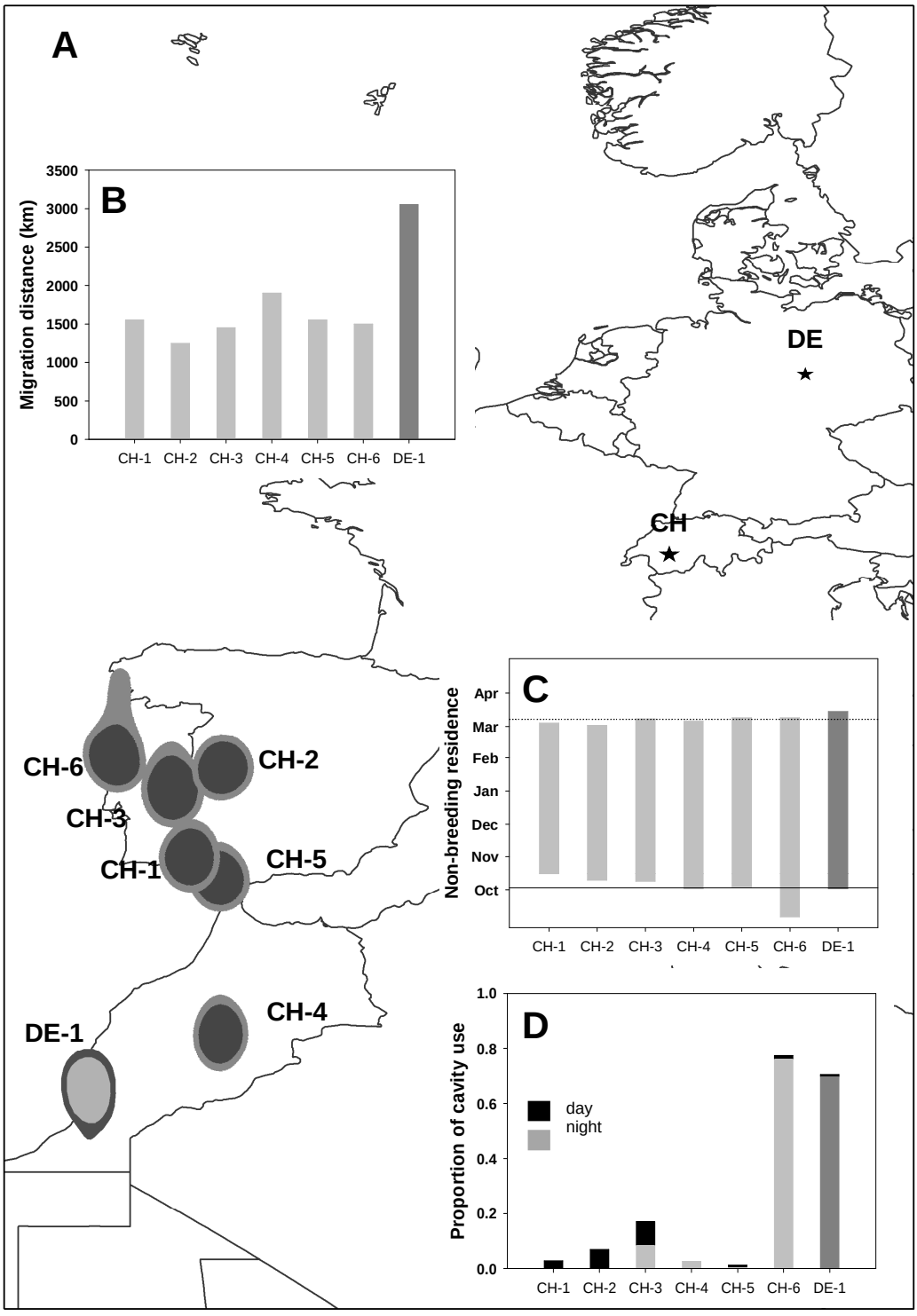

Figure 1. A) Overview of the non-breeding areas (depicted as 80% & 90% kernel densities) used by the 6 Wrynecks from Switzerland (CH-x) and one from Germany (DE-1). B) Loxodromic distances between the breeding and non-breeding areas. C) Time spent in the non-breeding areas, horizontal lines indicate the mean date of arrival and departure of all 7 birds. D) Proportion of days the birds used a cavity during the non-breeding period divided by day and night.

During the non-breeding period, all individuals sometimes rested in cavities during the night and/or during the day as recorded by unnatural sun events when entering ('evening') or leaving ('morning') the cavity, usually for a few days only (Figure 1D). However, one Swiss bird and the German bird used cavities more intensively during 76% and 70% respectively of the nights in the non-breeding period.

Wing lengths differed significantly between the different populations (Kruskal-Wallis One Way Analysis of Variance on Ranks, $H = 296$, $df = 4$, $P = < 0.01$, Table 1 and supplementary material). The median wing length of local breeders from Norway was significantly longer compared to breeders from Germany and from Switzerland. Wing lengths of birds from Germany were in turn significantly longer than those from Switzerland. However, wing lengths of birds on passage in Switzerland and Mauretania significantly differed from local breeders from Switzerland and Germany, but not from breeding birds from Norway ($P < 0.05$, Dunn's pairwise comparison test).

Discussion

Our data showed that none of the seven Wrynecks tracked migrated to Sahelian Africa, which is in contrast to the current belief of the location of the non-breeding areas of central European Wrynecks (e.g. Cramp *et al.* 1985, Reichlin *et al.* 2009). Most birds from the Swiss population spent the boreal winter on the Iberian peninsula; only one bird was located further south in Morocco. The one bird from Germany migrated furthest to southern Morocco. Observations of Wrynecks in these specific regions and other areas around the Mediterranean Sea are common during the boreal winter. However, they have typically been assigned to the subspecies *Jynx t. tschusii* and/or *Jynx t. mauretanica*. Since it is difficult to distinguish these two subspecies from the nominate form *Jynx t. torquilla* in the field (without having the bird in the hand, see e.g. Brichetti & Fracasso 2007), subspecies assignment might be (partly) erroneous.

Zwarts *et al.* (2009) suggested, based on a correlations of a Sahelian precipitation index and changes in various Wryneck populations that Wrynecks might winter in Sahelian Africa. Reichlin *et al.* (2010) used a triple stable isotope assignment approach to determine wintering areas of Wrynecks from Germany and Switzerland that partly supported this view. Expected wintering areas for Wrynecks from Switzerland, however, were assigned to West Africa, and with a lower probability, northern Africa, the Iberian Peninsula as well as the Congo basin (Fig. 3 in Reichlin *et al.* 2010). Wrynecks of the German population were assigned with the highest probability to the Horn of Africa. Our results however did not match the proposed main wintering areas (Fig. 1A).

Table 1. Overview of wing lengths ('WL') of the nominate form *Jynx t. torquilla* from different breeding populations and on migration. Median wing length is given with the 25% and 75% percentile.

Period	Country	Coordinates	Median WL	25%	75%	group	n	Source
spring migration	Norway	60°N, 5.5°E	**89.5**	*89*	*90.9*	a	63	I
breeding	Germany	52°N, 13°E	**88.5**	*87.5*	*90*	b	239	II
			88.0				1	geolocator bird
breeding	Switzerland	46.1°N, 7.2°E	**87.0**	*85.7*	*87.9*	c	469	III
			87.4	*86.3*	*88.2*		6	geolocator birds
boreal winter	Mauretania	20.9°N, 11.6°W	**91.0**	*89*	*92.5*	a	78	III

Sources are I) Revtangen Ornitologiske Stasjon (T. Lislevand, pers.com.), II) D. Tolkmitt (unpubl. data) and III) Swiss Ornithological Institute. The letters in group (a, b, c) indicate different populations based on differences in wing length. Wings of breeding birds from Norway were significantly longer than wings of breeding birds from Germany and Switzerland, but not significantly different from birds on passage caught in Mauretania (Dunn's pairwise comparison test, $P = < 0.01$, see text for further information).

Zwarts *et al.* (2009) focussed their study on the Sahel zone as a wintering area for many species in general, and they probably did not relate conditions of many potential wintering sites to population developments to cross-check for alternative non-breeding strategies in Wrynecks. Similarly, Reichlin *et al.* (2010) determined a very broad potential wintering range for Wrynecks of Switzerland and Germany, mainly due to low geographical differences in stable isotopes in Sahelian Africa. A re-analysis using recently developed isotope cluster approaches (Hobson *et al.* 2012) might give more reliable results.

If the Wrynecks from our study sites migrated to Sahelian Africa, the minimum distance to be covered would have been around 4500km. The birds from Switzerland covered on average only one third of this distance, the bird from Germany two thirds. Wrynecks observed in Sahelian Africa might originate from more northerly populations, e.g. from Scandinavia, and therefore would have to cover much longer distances, supporting the idea of a leap frog migration (Reichlin *et al.* 2010). This should be reflected in morphological differences in their flight apparatus (e.g. as in Wheatears *Oenanthe oenanthe*, Förschler & Bairlein 2011). Thus, we would expect gradually increasing wing lengths from southern to northern Wryneck populations. We indeed found significant differences in wing length; Scandinavian breeding birds captured on migration in Norway have longer wings compared to birds breeding in Germany, which in turn are larger compared to breeding birds from Switzerland (Table 1, $P < 0.001$ with non-parametric test; Dunn's method of pairwise multiple comparison). In addition, no significant differences in wing length could be found between these Scandinavian breeders and migrating birds captured in Switzerland and migrants captured in Mauretania. Thus, birds on passage in Switzerland and in Mauretania match in size only with the Scandinavian breeders, strongly supporting our idea that Wrynecks breeding in Northern Europe surpass their conspecifics in Central Europe to migrate to Sahelian Africa, whereas populations from Central Europe stay in southern Europe/northern Africa. We furthermore found that at least two Wrynecks spent a considerable amount in cavities overnight (Fig. 1D). This behaviour, in combination with the finding that a similar resident area was used, shows that Wrynecks in their non-breeding areas apparently behave similarly compared to the breeding grounds.

Overall our results shed light on the presumed migration of the Wryneck. The current belief that all individuals of the nominate form *Jynx t. torquilla* are consistently long-distance migrants probably should be revised. Yet, there is clearly a need for more information from other Wryneck populations in order to fully support the leapfrog migration hypothesis. Such information is important for conservation, since several European Wryneck populations are declining (PECBMS 2012). Environmental conditions in Africa such as precipitation patterns in the Sahel zone (e.g. the Sahelian

rainfall index, Zwarts *et al.* 2009) are unlikely to affect all European populations, and thus the causes might be originating elsewhere.

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CHAPTER 4 – HABITAT PREFERENCES OF WINTERING WRYNECKS (JYNX TORQUILLA) IN THE NORTH OF EXTREMADURA, SPAIN

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Submitted at Ardeola

Abstract / Resumen

The Iberian Peninsula is a well-known wintering area with an estimated 300 million birds wintering here each year. Most insectivorous birds winter in the southern part of the Iberian Peninsula where mild temperatures mid-winter ensure the availability and activity of insects. But case studies on specific species are still rare. One species of particular interest is the Eurasian Wryneck (*Jynx torquilla*). It's the only migratory woodpecker in Europe that feeds almost exclusively on ants and it has undergone declines throughout Europe over the past decades. Wrynecks are known to winter on the Iberian Peninsula, but only recently it was shown using geolocator data that at least some of these birds originate from Central European breeding populations. Still, it is unknown exactly what habitats these birds prefer, which likely are specific given their strong preference for ants as main food source. We studied the habitat preferences of Wrynecks in the Northern Extremadura, Spain, and found that they preferred diverse, extensive, agricultural (irrigated) croplands. More research is needed to find out whether these wintering Wrynecks found in the Northern Extremadura indeed (in part) originate from Central European populations, but our findings highlight the importance of this disappearing landscape for wintering migratory birds.

La Península Ibérica es una conocida área de invernada con unos 300 millones de aves estimadas pasando el invierno aquí cada año. La mayor parte de las aves insectívoras invernan en la parte sur de la Península Ibérica, donde unas temperaturas suaves e inviernos benignos aseguran la disponibilidad y actividad de los insectos. Una especie de particular interés es el torcecuello eurasiático (*Jynx torquilla*). Es el único pájaro carpintero migrador de Europa, que se alimenta casi exclusivamente de hormigas y ha sufrido declives poblacionales en toda Europa durante las últimas décadas. Se conoce que los torcecuellos invernan en la Península Ibérica pero sólo recientemente se ha demostrado, utilizando geolocalizadores, que al menos algunas de estas aves son originarias de poblaciones reproductoras de centroeuropa. Aún así, se desconoce exactamente qué habitats prefieren estas aves, que deben ser específicos dada su fuerte preferencia por las hormigas como su principal fuente de alimento. Las preferencias de habitat de los torcecuellos fueron estudiadas en el norte de Extremadura, España, resultando que seleccionaron heterogéneos y extensivos cultivos de regadío. Se precisa de más esfuerzo para aclarar si estos individuos invernantes encontrados en el norte de Extremadura proceden de poblaciones del centro de Europa, pero los resultados actuales subrayan la importancia de este paisaje en retroceso para la aves migratorias invernantes.

Keywords: Extremadura; Maxent; presence data; species distribution modelling; wintering distribution; wintering habitat.

Introduction

Roughly 300 million birds winter on the Iberian Peninsula (Santos and Telleria 1985), especially in the southern part of the Peninsula classified as Meso- or Thermomediterranean with relatively high mean temperatures during mid-winter and low precipitation (Santos and Telleria, 1985). The higher temperature ensures the availability and activity of insects throughout the winter months. Additionally, there are many (irrigated) croplands in this region, which are presumed to be the most preferred habitat for birds that are not bound to dense (oak) forests (Tellería et al., 1988).

One species of particular interest, is the Eurasian Wryneck (*Jynx torquilla*). Wrynecks are migratory woodpeckers with populations from Central, North and Eastern Europe presumably being sub-Saharan long-distance migrants, whereas birds from southern Europe and northern Africa are mostly short-distance migrants or resident (Cramp et al., 1985). Already in 1956 however, it was suggested that some birds found in winter on the Iberian Peninsula could actually be migrants from Central European populations (Moreau, 1956). Later studies however classified most wintering Wrynecks on the Iberian Peninsula as belonging to the subspecies *J.t. tschusii*, a partial migratory subspecies from the Mediterranean area, or *J.t. mauretanica*, a resident subspecies from northern Africa (Bernis, 1966). Any bird belonging to the nominate subspecies, was presumed to be local breeder (but see Reichlin et al. 2009). Only very recently it was confirmed that at least a part of the nominate species of Wrynecks that winter on the Iberian Peninsula, originate from Central European populations using geolocator data (van Wijk et al., 2013). Where exactly they occur in winter is however not clear to date, but during the breeding season Wrynecks almost exclusively feed on ants and occur in ant-rich habitat such as orchards and fallow land with sufficient bare ground for foraging (Mermod et al., 2009; Weisshaupt et al., 2011). We expected them to use similar ant-rich habitats within the Iberian Peninsula in winter. Based on the geolocator findings (van Wijk et al., 2013) and distribution predictions from the wintering atlas of Spain (SEO/Birdlife, 2012), we studied the habitat preferences of wintering Wrynecks in the northern Extremadura, Spain.

Material and Methods

We sampled 68 random locations throughout the Northern Extremadura during January 2014 and 2015 (Fig. 1). Locations were chosen by driving for a fixed amount of time over roads distributed through all the territory. At each of these locations we used playback using a Foxpro® Wildfire 2 (~100dB) for three minutes and subsequently waited five minutes for a response. Wrynecks are known to strongly respond to the songs of conspecifics, at least during spring and summer (Coudrain et al. 2010).

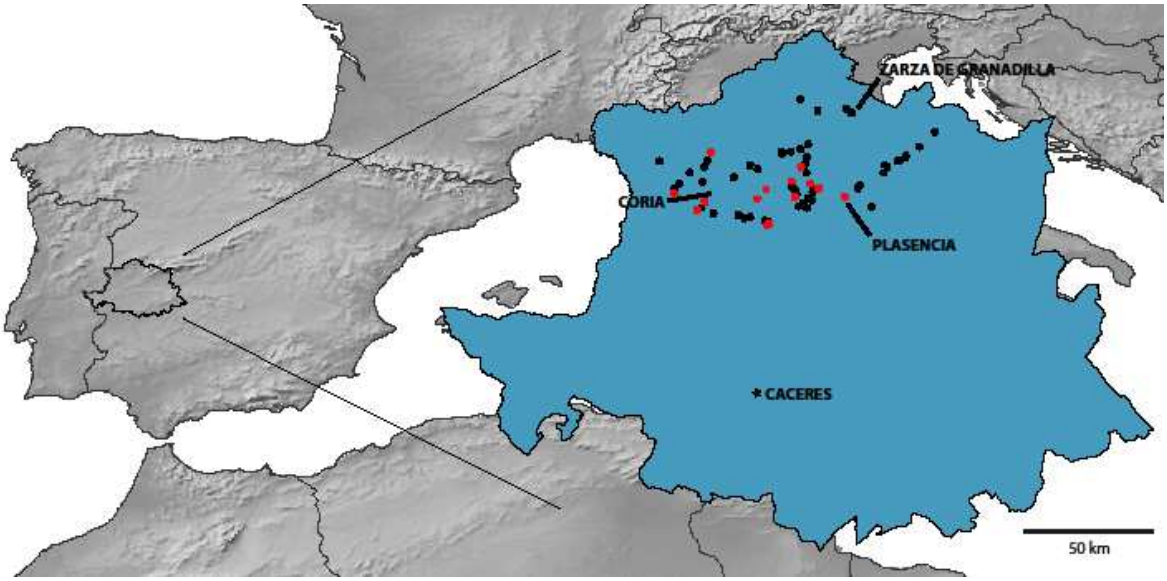

Figure 1. Overview of the study area and the locations that were sampled for the presence of Wrynecks in the Caceres Province, Northern Extremadura. The squares indicate 10 km^2 atlas squares from the wintering atlas project, colours showing probabilities of presence calculated by SEO/BirdLife 2012 (map adapted). Red dots show locations with confirmed presence, whereas in locations depicted with blue dots wrynecks were not detected.

To describe the habitats within this region, both in terms of bio-climate and environment, we used data of a wide range of variables which were acquired via a free access point, the "*Catálogo de Ministerio de Agricultura y Medio Ambiente*" (Table 1). Raster layers of 45.000km^2 were created for each variable with a pixel size of 60m^2 using QGIS (Quantum GIS Development Team, 2015). Since altitude is highly correlated with temperature and precipitation in the Iberian Peninsula (Lautensach 1967, Sa-Sousa 2000) only altitude was analysed as a climatic variable.

Subsequently we developed a model in MaxEnt using the 15 points where Wrynecks were present (Fig. 1), all available environmental layers (described in Table 1) and 10.000 random points throughout the 45.000km^2 area (Phillips et al., 2006). All environmental layers that did not contribute to the model were excluded (lambda of 0), after which each selected categorical layer was decomposed into different predictor variables, as many as categories, with a presence-absence format (1-0) (eg., presence of sclerophyllous forest). These categorical variables were tested for collinearity and layers with a correlation ≥ 0.70 or ≤ -0.70 were excluded. The selection of variables used in the final MaxEnt model, are described in Table 2. Variables were considered relevant for the interpretation of the model based on the outcomes of the jackknife test as part of the MaxEnt output: when at least percent contribution or permutation importance were > 1%, it was used to discuss the biological implications of the results (Table 2).

Table 1. Environmental variables used in the initial MaxEnt model, their general description, the number of categories within the variable layer (#Cat.), whether the layer was preselected in the initial MaxEnt model (Presel.), the number of categories of each environmental variable that were kept in the final model (#Cat. Kept) and the source of each environmental variable (Source).

Layer	Description	#Cat.	Presel.	#Cat. kept	Source
aguassub	underground water	1	no		IDEE MAGRAMA [1]
altitude	altitude (meters above sea level)	NA	yes	NA	Atlas climático digital de la Península Ibérica [2]
cauces	water course	1	no		IDEE MAGRAMA [1]
corinegeneral	generic land use, e.g. agriculture	4	yes	0	Corine Land Cover [3]
corine	specific land use, e.g, dry farming	26	yes	3	Corine Land Cover [3]
geopb	geological soil type	24	yes	1	IDEE MAGRAMA [1]
mfe50def	dominant vegetation	26	yes	2	Mapa Forestal de España. IDEE MAGRAMA [1]
mfe50nomforarb	structure of the forest	33	yes	1	Mapa Forestal de España. IDEE MAGRAMA [1]
mfe50usos	management of the habitat	7	yes	2	Mapa Forestal de España. IDEE MAGRAMA [1]
seriep	specific phytoclimatic classification of the vegetation	11	no		Mapa de Series de Vegetación. IDEE MAGRAMA [1]
seriepgeneral	generic phytoclimatic classification of the vegetation	7	no		Mapa de Series de Vegetación. IDEE MAGRAMA [1]

[1] Catálogo de Metadatos del Ministerio de Agricultura y Medio Ambiente de España. http://www.magrama.gob.es/ide/metadatos/

[2] Ninyerola M, Pons X & Roure JM. 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. ISBN 932860-8-7. Universidad Autónoma de Barcelona, Bellaterra.

[3] Centro Nacional de Información Geográfica. Instituto Geográfico Nacional. http://centrodedescargas.cnig.es/

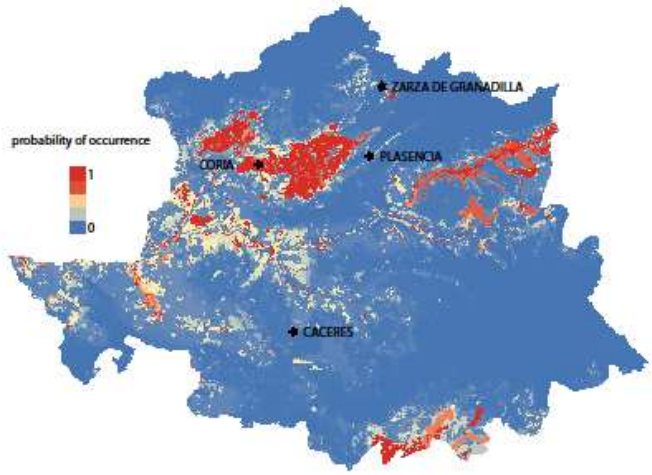

Figure 2. Predicted probability of occurrence of Wrynecks in the Caceres Province, Northern Extremadura following the MaxEnt output.

Results

The highest probability of Wryneck occurrence according to the final MaxEnt model (Fig. 2), is associated with habitats characterized by irrigated crops close to water bodies, with sparse woodland in the surroundings (Table 2). This is locally represented by extensive crops in soils characterised as riverbeds (predominantly sandy), where sclerophyllous vegetation adds structural diversity to the landscape. Other habitat features present in the areas highlighted in the final MaxEnt model, are crops like meadows or rice fields, as well as olive trees.

There was a strong influence of altitude on the probability of Wryneck occurrence. Wrynecks preferred lower altitudes which can be interpreted as warmer, drier locations with Mediterranean vegetation.

Interestingly, Wrynecks did respond to playback in mid-winter and thus seem to show some sort of territorial behaviour.

Table 2. The categories that were kept in the final MaxEnt model, their description, lamba, relative contribution and permutation importance. For more info, see text.

Layer	Description	Lambda	Percent contribution	Permutation importance
corine20	irrigated crops, e.g. rice fields	2.36	54.9	15.9
geopb24	geomorphological alluvial plain with gravel, clay	0.89	10.7	1.6
altitude	altitude (meters above sea level, range 7 – 232 meters)	-26.87	10.3	64.4
mfeusos6	cultivated areas	1.29	8.3	4.2
mfeusos2	forest	0.56	5.0	0.7
corine10	natural water bodies, e.g. rivers or ponds	3.74	3.4	2.3
corine13	sclerophyllous vegetation, e.g. *Quercus ilex*	1.80	2.2	2.0
mfe12	sparse woodland, e.g. patches of forest	1.05	1.7	0.2

Discussion

Based on the interpretation of the final MaxEnt model, we argue that wintering wrynecks preferred a mix of habitats corresponding to a diverse cropland, with an extensive management. Presence of scarce woodland provides shelter and presumably deep sandy soils, as those found in riverbeds, provide foraging opportunities (Tagmann-Ioset et al. 2012). Wrynecks in winter thus most likely occur in habitats in the vicinity of rivers with plain areas nearby, cultivated with irrigated crops, and some woody elements like scarce oaks, olive trees or big shrubs. These results indicate that wrynecks in winter use a very similar habitat as found in their breeding grounds (Martí and del Moral 2004, Weisshaupt et al. 2011). It thus appears that wrynecks are dependent on agricultural landscapes throughout their annual cycle.

The use of spatial distribution models to inform and predict the occurrence probability and habitat preference of a wide range of animals, has increased dramatically since the introduction of MaxEnt (Phillips and Dudík, 2008; Dormann et al., 2012). It is easy to use and interpret and results can be generated with few data. The habitat predictions we obtained from the MaxEnt model seemed to correspond well with was observed in the field. Nonetheless, the method has its drawbacks, most notably that it only uses the presence points (Yackulic et al., 2013) and disregards information from locations were Wrynecks were not found.

Information on absence points could be very useful and is incorporated in other modelling approaches like occupancy modelling (Beale and Lennon, 2012). For these kind of models however two observations per point are necessary since an observation probability has to be calculated. They are thus more data demanding and it would need more on the ground research to satisfy the requirements and compare the outcomes with the approach we followed using MaxEnt. Though given the apparent very specific habitat requirements of Wrynecks in our study area, it is unlikely outcomes will differ strongly, but it may allow for a more robust predictive assignment of the distribution of wintering Wrynecks on a broader scale, e.g. the whole Iberian Peninsula.

Another point is whether the wintering wrynecks observed are in fact migratory or resident birds. Such questions may be solved using wing morphology measurements (van Wijk et al., 2013) or isotopes (Hobson et al., 2009) or a combination of both. Given that birds responded to playback in winter, could suggest that the birds we observed are territorial and resident. But it could also relate to song improvement as was found in warblers wintering in Africa (Sorensen et al., 2015).

The origin of these birds and the nature of their presumable territorial behaviour mid-winter are thus still unclear, but in line with previous findings on wintering birds in the Iberian Peninsula, it

highlights the importance of extensive, agricultural landscapes in the Extremadura region (Navedo et al., 2015). Given intensification of agriculture, these landscapes are under pressure of disappearing. Future conservation efforts in these regions should be directed to their sustainable maintenance, not only for wintering birds, but also many breeding birds of international conservation concern.

Acknowledgements

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CHAPTER 5 – INDIVIDUAL MIGRATION ROUTES, WINTERING SITES AND TIMING ARE REPEATABLE IN A LONG-DISTANCE MIGRANT BIRD – AT LEAST TO SOME DEGREE

Rien E. van Wijk, Silke Bauer & Michael Schaub

In preparation for Ecology and Evolution

Abstract

Migratory birds are often faithful to wintering (non-breeding) sites and also migration timing is usually remarkably consistent. Spatio-temporal repeatability can be an advantage because it ensures familiarity with local resources and predators and avoids the costs of finding a new place. However, when the environment is variable in space and time, variable site selection and relaxed timing might be more adaptive. To date, studies on spatial and temporal repeatability in long-distance migrants are scarce, most notably of first-time and subsequent migration. Here we investigate repeatability in autumn migration directions, wintering sites and annual migration timing in individual Hoopoes (*Upupa epops*), a long-distance migratory near-passerine, using repeated tracks of adults and first-time migrants. Even though autumn migration directions were mostly the same, wintering sites often changed from year to year within individuals. The timing of migration was consistent within an individual during autumn, but not during spring migration. We suggest that Hoopoes are strongly affected by variable environmental conditions during wintering and spring migration. They likely change wintering sites to profit from unpredictable food resources in the Sahel region and adapt their spring timing according to changing environmental conditions.

Introduction

Many bird species are faithful to their breeding grounds (Greenwood 1980). Site fidelity can be advantageous because of familiarity with local resources and predators (Greenwood 1980, Part 1991, Piper 2011) while searching for a new site may cost energy and increase predation risk (Yoder et al. 2004). In migratory birds, site fidelity may not be restricted to breeding grounds, but can also apply to wintering (non-breeding) and stopover sites (Phillips et al. 2005, Vardanis et al. 2011, López-López et al. 2014, Senner et al. 2014, Yamamoto et al. 2014). Migrants can also show consistent annual timing when site fidelity is high (Vardanis et al. 2011, Conklin et al. 2013). Birds that adopt spatially and temporally consistent migrations often depend on particular resources that are exclusively available at specific places and times. For example, shorebirds depend on food-rich mudflats, seabirds follow sea currents, or raptors need specific wind and thermal conditions for migratory progression (Berthold 2001, Newton 2008). When birds depend on such particular conditions, they are forced to follow a rigid migration strategy that results in high site fidelity and temporal repeatability.

Contrastingly, other migrating species rely on resources whose availability is variable in time and space (Andersson 1980, Schlossberg 2009). The best strategy then would be to adopt a flexible migration strategy responding to environmental conditions during migration and in the wintering sites. Many (near)passerines are likely to use such a flexible strategy, yet empirical evidence is scarce. Catry et al. (2004) showed for passerines stopping over in spring that site fidelity was low, probably caused by flexible strategies to cope with winds during migration whereby birds end up on different stopover sites each year. Similarly, Stanley et al. (2012) showed for Wood thrushes (*Hylocichla mustelina*) that both autumn and spring migration routes differed within individuals from year to year, likely because of changes in weather.

In this study, we investigated the repeatability of autumn migration directions, migration timing in autumn and spring and the location of wintering sites for subsequent migrations in a near-passerine: the Hoopoe (*Upupa epops*) using geolocator data of both first-time and adult migrants.

Material & Methods

Study site and data collection

Our study was conducted in a population of Hoopoes in southern Switzerland (46°14'N 7°22'E). Prior to our study, ~700 nestboxes were installed in the roughly 62km^2 study area (Arlettaz et al. 2010a). To investigate the autumn migration directions, migration timing and wintering sites, birds were equipped with geolocators of type SOI-GDL1 (Bächler et al. 2010). These geolocators comprise a weight of <2% of the body weight of a Hoopoe and were shown to affect neither body condition,

physiological state, breeding success nor annual apparent survival (van Wijk et al. 2015b). Between 2009 and 2014, 328 breeding birds and 459 nestlings were equipped with geolocators. We retrieved geolocators in the breeding grounds and obtained migration data of 10 adults over two years, two adults over three years and six first-time migrants ('juveniles') during their first and subsequent migration.

Migration data

Geolocator data were analysed as described in van Wijk et al. (2015a). This procedure used the *TrendLight* function in R (Schmaljohann et al. 2015) to define stationary periods, which were required to describe the timing of i) departure date from the breeding grounds, ii) arrival date in the wintering sites, iii) departure date from the wintering sites, iv) arrival date in the breeding grounds and the duration of autumn and spring migration. The wintering site was defined as the first site, where birds stayed for at least six weeks after leaving the breeding grounds. Positions were calculated for the period November until January to avoid influence of equinox and to keep the method comparable between birds. In few occasions, we found multiple wintering sites, and consequently the position of the first site was calculated from 1st of November until departure and the position of the second site from the arrival until 31st of January. We calculated positions using site-specific sun elevation angles for each wintering site (varying between -3 and -7) using the HillEkstrom method within the R-package *GeoLight* (Hill 1994, Ekstrom 2004, Lisovski and Hahn 2012). From the combined final positions of each wintering site, kernel densities were calculated using ArcGIS and the 25% kernel was kept for further analysis. For one adult, we lacked sufficient positions in winter, likely caused by temporary battery problems, which resulted in data gaps and unnatural sun events.

We only investigated autumn but not spring migration routes, since we had too few data in spring and some geolocators had stopped recording before birds returned to the breeding grounds. In order to investigate autumn migration directions, we used longitude data after departure from the breeding grounds and established whether birds had used a route via a) the Iberian Peninsula, b) islands in the Western Mediterranean Sea or c) mainland Italy. We used this coarse classification of autumn migration directions to overcome problems with positioning during equinox.

Data analysis

To determine whether individuals had used the same wintering site, we had to account for the uncertainty of the position-estimates from geolocator data (Lisovski et al. 2012). Here, a distance of >0 kilometres between two wintering sites could result when an individual had actually changed wintering sites but could also result from uncertainty around the estimated positions. Therefore, we quantified the uncertainty assuming the wintering site had remained unchanged with the following

procedure: For a conservative uncertainty estimate, we used a maximal geolocator uncertainty of roughly 350 km in latitude and 150 km in longitude, based on Fudickar et al. (2012). We generated two random points within a rectangle of 150 x 350 kilometres, calculated the distance between them, and repeated this 10.000 times. The density distribution of the resulting distances delimit the distances under which we cannot distinguish whether or not wintering sites have changed. The distances between wintering sites within individuals were calculated using the great circle distances. In case of multiple wintering sites within the same season, we used the first site. If the observed distances between wintering sites were larger than this geolocator uncertainty distance, we assumed wintering sites have changed, while for observed distances below this threshold wintering site fidelity was *likely*.

To test whether first-time migrants spread out over a larger area than adults, we compared the surface area encompassing 70% of the wintering sites using the Standard Deviational Ellipse tool in ArcMap 10.0.

To test the repeatability of migration timing, we used the intra-class correlation coefficient (ICC, Lessells and Boag 1987) using the package ICC in R (Wolak et al. 2012). Since the timing of adult and first-time migrants in Hoopoes does not differ (van Wijk, *unpubl.*), we combined data of both age classes to increase the sample size.

Results

Both adult and first-time migrants spread out over a vast area throughout western Africa (~2000 kilometres West-East, Fig. 1), and the majority of birds used the same autumn migration direction each year. In adults, roughly 69% followed the same direction and 75% of first-time migrants repeated their direction as adults (Table 1). Individuals that changed autumn migration directions usually switched to a faster route via islands in the Western Mediterranean Sea (80% of cases; Table 1, cf van Wijk et al. 2015a).

The simulated geolocator uncertainty distribution indicated that for distances up to 375 km we cannot distinguish individual wintering sites (Fig. 2). Taking this uncertainty into account, about 45% of the adults wintered in the same site while 55% changed wintering sites between years (Table 1 and Fig. 1). Half of the first-time migrants wintered in the same site in the subsequent year (Table 1 and Fig. 1).

First-time migrants distributed over a larger area compared to adults (2.1 million km^2 versus 1.7 million km^2 respectively), while the distances between wintering sites within individuals did not differ between these groups (Kruskal Wallis rank sum test $P > 0.05$; median of 319 ± interquartile range of 329km in first-time migrants, N = 6 versus 411 ± 404km, N = 13 in adults, see also Fig. 1).

Table 1. Overview of individuals in the analysis on spatial repeatability of migration indicating which autumn migration directions were used in the first year of tracking (y 1) and subsequent years (y 2, y 3); whether birds likely used the same wintering sites (Likely) or not (Not); the distances between wintering sites (rounded to the nearest 25km); the number of wintering sites in a season; and which colour corresponds to which individual in Figure 1. Autumn migration directions were either via the Iberian Peninsula (Iberia), islands between the Iberian Peninsula and mainland Italy (Islands) or mainland Italy (Italy). – indicates there was no data available. Age refers to the age at the first autumn migration.

age	**sex**	**year**	**ring**	**autumn migration directions**			**wintering sites same**		**site distances (km)**		**# wintering sites**			**colour Fig. 1**
				y 1	*y 2*	*y 3*	*1 – 2*	*2 – 3*	*1 – 2*	*2 – 3*	*y 1*	*y 2*	*y 3*	
adults	M	2009	H107445	Iberia	Iberia	Iberia	Not	Likely	575	125	1	1	1	Light green
	F	2009	H107459	Islands	Iberia	Islands	Likely	Likely	100	175	1	1	1	Dark blue
	M	2009	H107582	Iberia	Iberia		Not		450		2	2		Dark green
	M	2010	H110718	Iberia	Iberia		Likely		250		1	1		Pink
	F	2010	H110911	Iberia	Iberia		Not		1300		1	1		Grey
	F	2011	H111115	Iberia	Iberia		Not		400		1	1		Blue
	F	2011	H111176	Iberia	Islands		Likely		325		1	1		Light blue
	M	2011	H115004	Iberia	-		Not		650		1	1		Purple
	M	2011	H77452	Islands	Islands		Not		975		1	1		Brown
	F	2012	H117910	Iberia	Islands		Not		525		1	2		Orange
	F	2012	H117873	Islands	Islands		-		1125		-	-		-
	M	2013	H44866	Iberia	Iberia		Likely		75		1	1		Red
juveniles	F	2012	H102456	Islands	Islands		Likely		175		1	1		Green
	M	2012	H117732	-	Islands		Not		500		1	1		Blue
	M	2012	H44866	-	Iberia		Likely		150		1	1		Red
	F	2013	H117935	Islands	Islands		Not		475		1	1		Yellow
	F	2013	H121128	Iberia	Iberia		Not		600		1	1		Purple
	F	2013	H121752	Italy	Islands		Likely		50		1	1		Orange

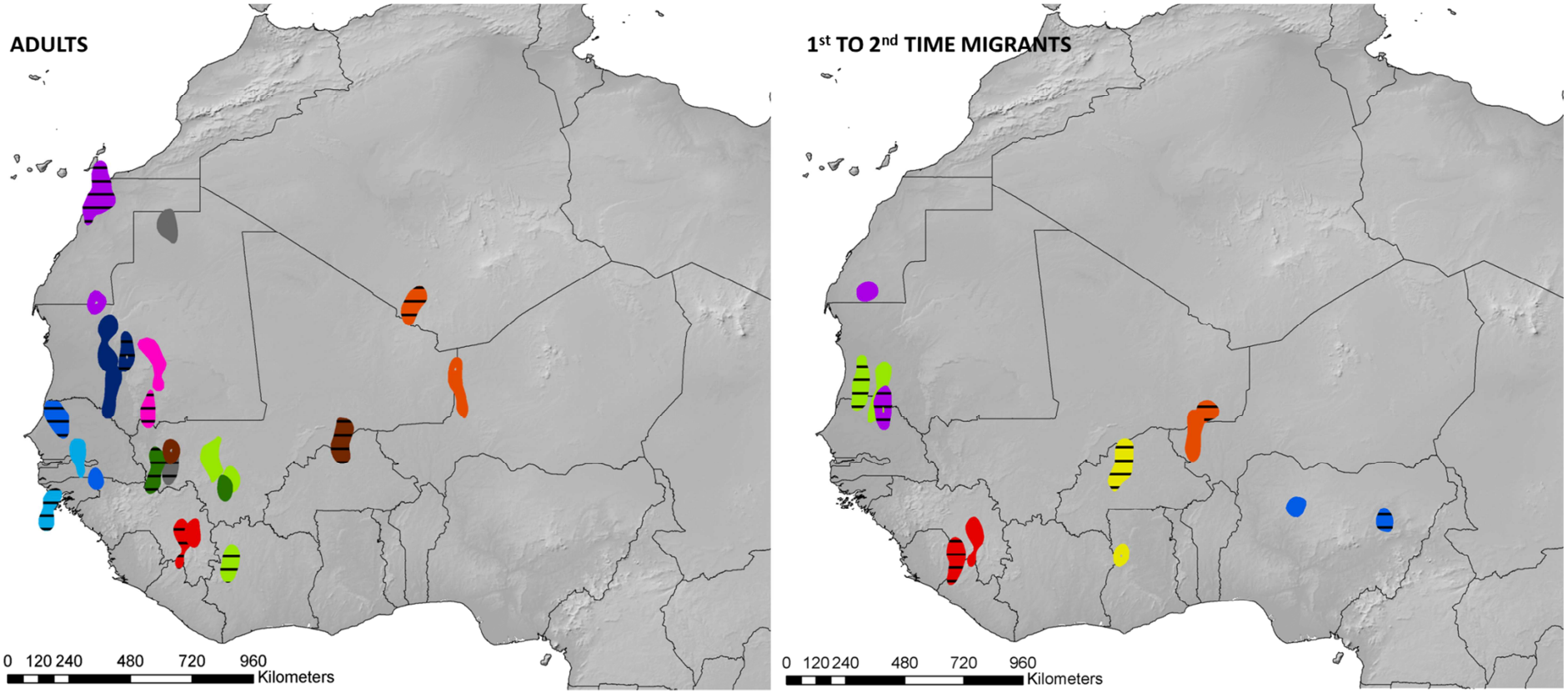

Figure 1. Wintering sites of adult and first-time migrants as represented by 25% kernels based on position data for the months November until January. In the case of multiple wintering sites, only the first is shown. Each colour-patch represents the wintering site of one individual (see Table 1) with barred patterns referring to the wintering sites in the first migration recorded.

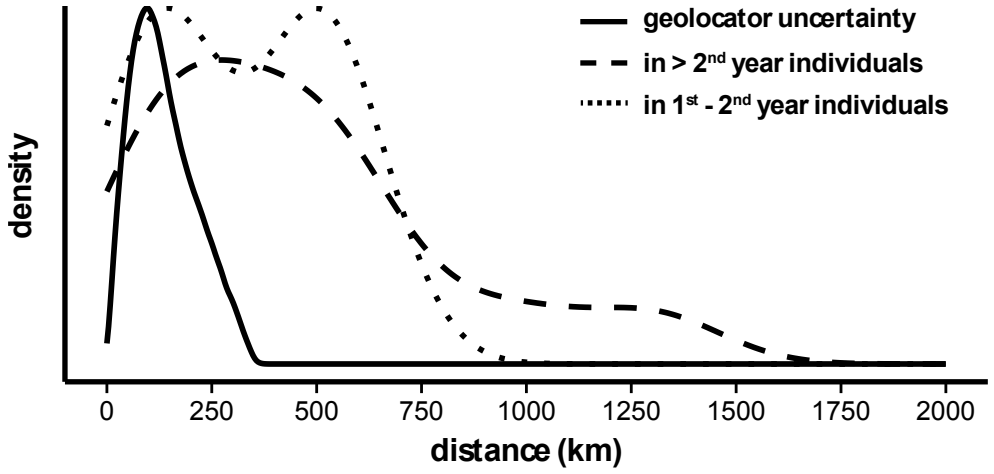

Figure 2. Density distribution of distances between wintering sites in adult (≥ 2nd year individuals) and first-time migrants (1st to 2nd year individuals), together with the distribution of uncertainties inherent to geolocator position estimates.

Timing of migration was highly repeatable for departure from the breeding grounds and arrival in the wintering sites (Figs. 3a & 3b), and moderately repeatable for the duration of autumn migration (Fig. 3c). In contrast, temporal repeatability was low for departure from the wintering sites and arrival in the breeding grounds (Figs. 3d & 3e), and consequently also for the duration of spring migration (Fig. 3f).

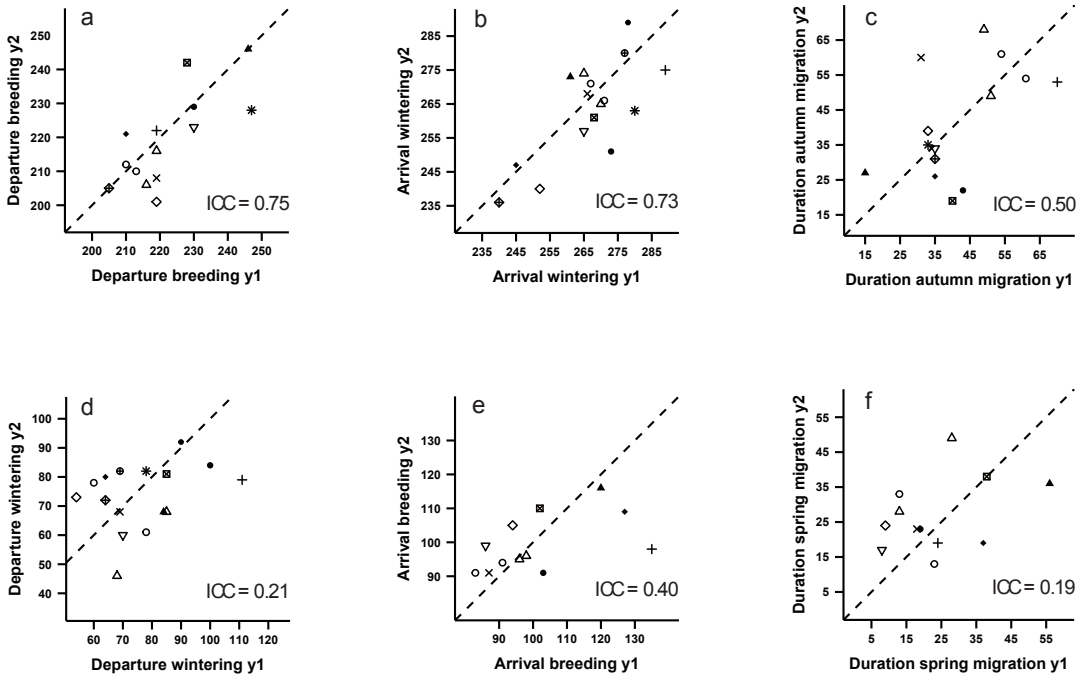

Figure 3. Repeatability of timing between successive individual migration bouts for adult (open symbols) and first-time migrants (closed symbols). The dashed line represents the highest achievable repeatability score (ICC) of 1, i.e. when individuals would have used the same timing in successive migrations, and for comparison, the data-derived ICC is provided. symbols indicate individuals.

Discussion

We found that both the majority of adult and first-time migrants changed wintering sites from year to year following the same autumn migration directions whereby first-time migrants spread out over a larger area. Repeatability of timing was high during autumn, but not during spring migration.

Autumn migration directions were repeatable in both first-time and adult migrants, which suggests that after their first migration, individuals repeat the general route that had been proven successful in the previous year. We deliberately choose the term “directions”, since we did not investigate finer-scale movements, e.g. specific stopover site use. The exact location of stopovers may have changed between years in which case repeatability would have likely appeared to be lower (Catry et al. 2004).

The low wintering site fidelity we found could partly be influenced by our methodology. For instance, if we change the threshold distance that determines whether or not birds had used the same wintering sites, this would also result in changes to site fidelity: decreasing the threshold distance would decrease wintering site fidelity, while increasing it would increase site fidelity. We used a relatively high threshold (see e.g. Lisovski et al. 2012), implying that distances between wintering sites had to be relatively high to be defined as ‘different’. Changing the position estimates for the wintering sites, e.g. by fixing the sun elevation angle, could also have altered the resulting site-fidelity. A fixed sun elevation angle would have shifted sites over a North-South gradient, but the location of wintering sites between years would have changed to roughly the same extent along this North-South gradient within an individual and thus the absolute distance between wintering sites would have hardly changed. It is therefore most likely that hoopoes indeed typically changed wintering sites between years.

Even though specific sites thus changed, birds did show fidelity to a general region and for instance did not winter at the Atlantic coast in one year and in inland Niger the next year. Being bound to a certain region restricts the extent of their movements in winter in West-Africa, within which birds do change the exact location of their wintering sites. To the contrary, in species that are known to be territorial during winter, it was shown that individuals returned to almost the exact same spot each winter (Salewski et al. 2002, Blackburn and Cresswell 2015). Defining fidelity thus in part depends on the definition: in hoopoes there seems to be more fidelity on a larger, regional scale.

A more flexible strategy for wintering site selection might be adaptive with respect to the environmental circumstances in West-Africa. These vary greatly from year to year, predominantly under the influence of the Inter Tropical Convergence Zone (ITCZ or ITF, Intertropical Front; Lélé &

Lamb, 2010). Depending on the northward spread of the ITCZ, the precipitation pattern varies likewise up to several hundreds of kilometres North-South between years (Lélé and Lamb 2010). Therefore birds may be able to profit in some years from habitats that are usually dry, such as wadis (Hall 1976, Giradoux et al. 1988), whereas in other years they have to migrate much further south to find suitable habitat.

Next to that, in some years, outbreaks of Desert locusts (*Schistocerca gregaria*) may occur, especially in the northern region of the Sahelian zone in West-Africa, (Lecoq 1978, Tratalos et al. 2010). Locusts are known to be an important food source for wintering migrants (Stoate 1995, Trierweiler et al. 2013), yet their outbreaks are hard to predict (Tratalos and Cheke 2006). Although the exact diet of hoopoes in winter is unknown, their typical diet includes large soil invertebrates (e.g. Mole crickets on their breeding grounds; Fournier and Arlettaz (2001)), suggesting that they would include locusts in their diet if these were available.

The combination of both environmental stochasticity and (partly related) food availability, could well explain changes in exact wintering sites between years within an individual, which strictly speaking would result in apparent low wintering site fidelity.

Compared to adults, first-time migrants spread out over an intriguingly larger wintering area. We found no apparent differences in autumn migration directions that could explain this, but first-time migrants might have responded differently to environmental conditions upon approaching their final wintering site. For instance, wind might have caused them to drift more and spread over a larger area (Thorup et al. 2003) and they might still be inexperienced as to in which habitat they should stay (Battley 2011). As a consequence, they might have ended up in other, sub-optimal habitats compared to adult migrants. A larger spread of wintering sites may also result from an active exploration behaviour whereby they end up in different sites, further apart, compared to adult migrants (Battley 2011). In the long-term this might be advantageous when they e.g. identify new suitable sites (and thereby e.g. increase carrying capacity of the population), which has been termed the serial residency hypothesis (Cresswell 2014). But it would require individuals to show high fidelity to these sites. Strict winter site fidelity in Hoopoes however was relatively low, but as discussed before it depends on the scale. They could be faithful to certain regions or habitats in which case the hypothesis may still be applicable. More detailed data on the exact locations of wintering sites, habitat use and foraging behaviour within an individual would be needed to draw conclusions on whether the serial residency hypothesis applies to hoopoes.

Only very few studies to date have investigated the repeatability of the timing of autumn versus spring migration, but most have found that the timing of spring migration was more repeatable than

the timing of autumn migration (Stanley et al. 2012, López-López et al. 2014, but see Alerstam et al. 2006). In contrast to these expectations, we found the timing of autumn migration in Hoopoes to be relatively consistent, but not spring migration timing. Since (selective) pressure is probably not as strong for arrival in the wintering grounds as it is for arrival in the breeding grounds, birds migrate slower in autumn, spending more time on stopovers (Alerstam et al. 2006, Nilsson et al. 2013). As a consequence, environmental conditions hardly affect the duration of autumn migration (Schaub and Jenni 2001, Jenni and Kéry 2003, Pulido and Widmer 2005). Birds seem to be controlled by the individual's endogenous migration schedule and consequently repeatability of timing is high. To the contrary, spring migration is much more influenced by the environment (Sokolov and Kosarev 2003, Hüppop and Hüppop 2003, Saino et al. 2004, Both et al. 2005, Newton 2006, Balbontín et al. 2009). Additionally, birds are under strong selective pressure to arrive timely in the breeding grounds (Kokko 1999). The exact date of departure from the wintering sites thus likely varies from year to year depending on the local conditions, after which birds try to migrate as quickly as possible back to the breeding grounds to increase reproductive success (van Wijk et al. 2015a). Meanwhile individuals may have to adapt their timing between years to cope with environmental variability *en route* (Bauer et al. 2008, Balbontín et al. 2009). The differences in timing in response to yearly differences in environmental conditions will cause apparent low repeatability of timing within an individual during spring. The differences in selective pressures on timing and corresponding responses to environmental changes between autumn and spring likely explain the difference in repeatability of timing we found.

We conclude that hoopoes overall seem very flexible in migration timing and the choice of wintering sites and propose that they could be classified as opportunistic migrants with high fidelity to their breeding grounds (Bötsch et al. 2012).

Acknowledgements

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CHAPTER 6 – COMPENSATION IN A LONG-DISTANCE MIGRATORY BIRD:

THE WINTERING PERIOD WEAKENS DEPENDENCIES IN THE TIMING OF THE ANNUAL CYCLE

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In preparation for Behavioral Ecology

Abstract

Next to breeding and molting, migrating birds have to incorporate migration into their annual cycle. This presents the challenge to arrive at the right place at the right time to maximize fitness. Even though many studies have investigated the timing of specific seasonal activities in the annual cycle of migrating birds, it is yet poorly studied how timing events throughout the annual cycle depend on each other and, ultimately, how they affect reproductive success. This includes also the question when birds have room to compensate for delays by speeding up migration. We investigated these aspects in Hoopoes (*Upupa epops*) using a combination of geolocator and breeding phenology data of five consecutive years. We found that the timing of events generally depended on the timing of the preceding event, but least so for the timing of departure from the wintering grounds. Therefore, the potential for compensation was largest during the non-breeding period, which thus seemed to function as a reset in timing dependencies. Contrary to our expectations, arrival in the breeding grounds was more strongly related to the duration of spring migration, rather than solely on the departure from the wintering grounds. Finally, a later arrival in the breeding grounds led to a later onset of breeding and fewer fledglings.

Kewords: autumn migration, spring migration, reproductive success, geolocator, hoopoe, non-breeding

Introduction

Migrating birds face the challenge of having to time both breeding and migration during the annual cycle in such a way that they can optimally profit from (food) resources that are often only available during specific times and at specific places during the year (McNamara et al. 1998, Alerstam 2011). It is generally thought that compensation for mistiming, by reducing the duration between successive events, is limited and flexibility in timing low, especially during migratory progression.

Penalties for mistiming likely differ throughout the annual cycle and thus also selective pressures. For instance, selective pressure for arrival time is much lower on the wintering than on the breeding grounds, since the latter strongly correlates with reproductive success (Kokko 1999, Gienapp and Bregnballe 2012). As a consequence, spring migration is much faster compared to autumn migration in most migratory systems and occurs within a smaller time window (Nilsson et al. 2013). Likewise, the potential for compensation likely differs throughout the annual cycle.

Timing of migratory progression is most likely linked throughout the annual cycle, whereby, e.g., a late onset of autumn migration leads to a delayed arrival in winter. To understand migration strategies, it is thus crucial to understand the dependencies between timing events from the breeding grounds, on migration, to the wintering grounds and back to breeding grounds. Depending on whether these dependencies are strong or weak, this will allow us to identify and quantify moments in the annual cycle where birds could compensate for delays caused by, e.g., an extended breeding season, adverse environmental conditions or decreased body condition upon departure from the wintering grounds. This requires data on both migration and breeding phenology, which easily becomes a complicated endeavour. Therefore, most studies to date have focussed on the timing of particular parts of the annual cycle, mostly spring migration (Hüppop and Hüppop 2003, Jonzén et al. 2006, Tøttrup et al. 2010), occasionally also in relation to reproductive success (Weatherhead 2005, Gordo et al. 2013, Clausen et al. 2015). Studies that investigated the timing of the entire annual cycle, potential for compensation and its consequences on reproductive success are lacking to date.

Overall, we expect that the timing of consecutive events depends on each other and that the variability in the timing of these events differs over the course of the annual cycle. Furthermore, we also expect the potential for compensation to vary between timing events. Lastly, timing of events will also have fitness consequences, notably the timing of arrival in the breeding grounds should be correlated with reproductive success.

We investigated the timing of the annual cycle and its consequences on reproductive success in Hoopoes (*Upupa epops*), a near-passerine long-distance migrant, using geolocators. We first tested for differences in timing between sexes and subsequently tested the expectations introduced above.

Methods

Study population and study set-up

We conducted our study in a population of hoopoes that breed in southern Switzerland (46°14'N 7°22'E) and spend the wintering (non-breeding) season in the Sahel region of West-Africa (Bächler et al. 2010). The study area is roughly 62km^2, and approx. 700 nestboxes had been installed prior to this study (Arlettaz et al. 2010). To investigate the annual timing, their dependencies and consequences, we equipped birds with geolocators and recorded their reproductive performance.

We characterized the timing of the following key periods and events within the annual cycle (Fig. 1): a) *autumn migration* as delimited by the departure from the breeding grounds and arrival in the wintering grounds, b) *wintering* by arrival in, and departure from, the wintering grounds, c) *spring migration* by departure from the wintering grounds and arrival in the breeding grounds and d) the *breeding* period that started with the date of laying the first egg (onset of breeding) and ended when the last brood had fledged (*end reproduction*). We furthermore defined the *pre-breeding* period as the time between the arrival of a bird in the breeding grounds and the date when the first egg was layed and the *post-breeding* period as the time between fledging date of the last brood and departure (Fig.1).

Data collection

Between 2009 and 2014, we equipped 328 breeding hoopoes with geolocators of type SOI-GDL1 (Bächler et al. 2010). These geolocators, including a leg-loop harness, weigh on average 1.32g, which corresponds to roughly 2% of a hoopoe's body mass. In a previous study, no negative effects of these geolocators on body condition, physiological state, reproductive success or survival were found (van Wijk et al. 2015b). We retrieved 81 geolocators, 71 of which had usable data. When a particular individual was repeatedly equipped with a geolocator, we only used data from the first year of deployment, which left 57 geolocators. For 13 individuals the geolocators contained missing data and thus, incomplete annual cycles.

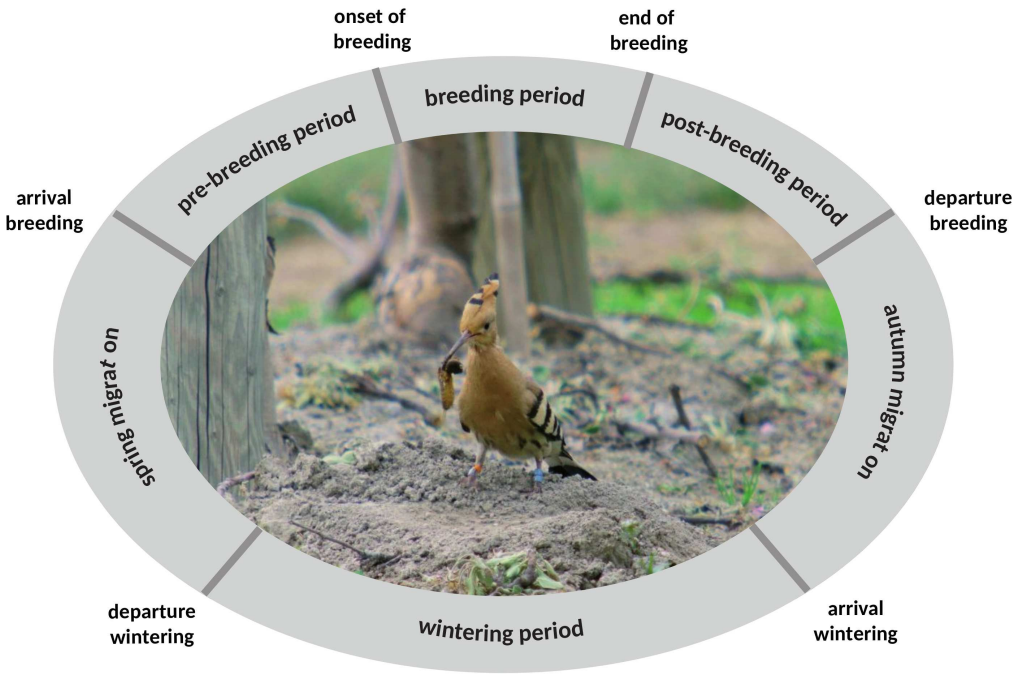

Figure 1. The annual cycle of a Hoopoe consists of several key periods (in boxes), which are delimited by timing events (outer variables). In our study the fledging date marks the start of the annual cycle.

We followed a step-wise procedure to identify stationary periods and their timing from light-level data, using functions of the package GeoLight (Lisovski and Hahn 2012) in combination with scripts described in Schmaljohann et al. (2015), both using R (version 3.1, R Core Team 2014). We first defined sun events from light level thresholds: sunrise as the time when this threshold was exceeded and sunset when light-levels fell below the threshold. Subsequently, we filtered 'false' sun-events, e.g. when birds entered or left the nestbox, using the *loessFilter* with k=2 and *runningMax* filter set to k=25. We defined stationary periods with the function *trendLight*, which uses the difference in sun events between successive days and is thus independent from location estimates. Since trendLight was set to be very sensitive for sun event changes, sometimes additional stationary periods were defined that actually belonged to the same site. To control for that, preliminary positions were calculated with a fixed sun elevation angle of -5°, and sites were merged when the modus of their positions were either <= 250 kilometers apart for the migratory period or <= 400 kilometers for the wintering period. Similarly, sites between the migratory and wintering period were merged when they were less than 400 kilometers apart. The migratory period was defined as the period from the start of recording until 14 October and from 16 February until retrieval of geolocators, and the wintering period as the period from 15 October until 15 February.

In order to detect site changes during migration, we used more sensitive filter settings during the migratory period. We used a window size of 13 backward- and forward-days and a minimum stationary period length of 2 days, compared to 11 backward- and forward-days and a minimum period length of 3 days for the wintering period.

The main wintering site was defined as the site where birds stayed for the longest time between October and February. Final positions were calculated within this wintering period using a sun elevation angle identified from a habitat calibration (Schmaljohann et al. 2015). In a few cases, individuals used two wintering sites on which they stayed at least two months between October and February. For these, we delimited the wintering period by the arrival in the first, and departure from the second wintering site.

We obtained data on breeding phenology and success of broods by regular visits to all nestboxes. Every 14 days, we checked all nestboxes in our study area, visited occupied nestboxes every third day to obtain dates for egg laying and hatching and the number of broods and fledglings per individual (see also Hoffmann et al. 2015). Fledging dates were defined as 28 days after hatching (Martín-Vivaldi et al. 1999). We used nestbox occupancy, i.e. the proportion of years a nestbox was occupied over the years it was installed, as a measure of territory quality (Tschumi et al. 2014). To characterize the timing of breeding and reproductive output, we used the date of the onset of breeding; the number of broods conducted; the number of fledglings in the first brood; the total number of fledglings; and the fledging date of the last brood.

If not stated otherwise, dates that delimit timing events are given as medians +/- the interquartile range.

Data analysis

To investigate dependencies between timing event events, we used linear fixed effects models with Gaussian-distributed residuals for each timing event. We fitted models with all possible combinations of explanatory variables (Table S1). All initial models included the timing of the preceding event and sex. Additionally, several models included measures of reproductive success, nestbox occupancy and duration of spring migration as explanatory variables. For the arrival in the wintering grounds, we also included the general autumn migration route. For the latter, we appointed birds to a route via either 1) the Iberian Peninsula, 2) islands in the western Mediterranean Sea or 3) mainland Italy based on the progression of longitude over time after departure from the breeding grounds. We also calculated the great circle distance from the breeding grounds to the modus of the (first) wintering site and included that in the model on the arrival in the wintering grounds as well. Finally, all models were run with and without year effect. We compared

the models using small-sample size corrected Aikaike Information Criterion (AICc) weights (R-package AICcmodavg, Mazerolle 2015).

We tested whether the variance in timing of the different timing events was equal between timing events and durations using Bartlett statistics (Bartlett 1937).

When the duration of a specific period is adjusted to a fixed finishing date (compensation), we would expect specific relations between starting date, duration and finishing date (Fig. 2). The three ideal cases are 1) full compensation, 2) an intermediate strategy or 3) no compensation. Under full compensation, we would expect the finish of a certain period to be fixed, regardless of the start of this period, and the duration to decrease with a later start, but to be independent of the finishing date (Fig. 2a). In the other extreme – no compensation - a later start of a period would always lead to a later finish and as such the duration between start and finish would be fixed (Fig. 2c). Finally, an intermediate strategy would imply that start and finish depend on each other to some degree, but the duration varies both with start and finishing date: a later finishing date is in part the consequence of a longer duration (Fig. 2b). To test which of these scenarios apply to specific periods, we compared these ideal cases to empirical data for which in a bootstrap procedure ellipses were calculated encompassing 70% of the data, using the function *Stat-ellipse* in R (version 3.1, R Core Team 2014).

Finally, to identify the fitness-consequences of timing, we used linear models to investigate whether arrival in the breeding grounds explained onset of breeding and reproductive success and additionally included sex and nestbox occupancy as explanatory variables.

Results

We found no significant differences in timing between adult males and females - they timed activities similarly throughout the year (Kruskal-Wallis test, $p > 0.05$ in all cases). The breeding season ended earlier in individuals with one breeding attempt (26 June ± 39 days, N = 29) compared to those with two (18 July ± 20 days, N = 23) or three brood attempts (26 July ± 11 days, N = 5). Autumn migration was initiated on 16 August ± 15 days and subsequent arrival in the wintering grounds was on 23 September ± 22 days, making the duration of autumn migration slightly more than one month (Table 1). Spring migration was conducted in roughly three weeks. Departure from the wintering grounds was on 10 March ± 15 days and subsequent arrival in the breeding grounds was 5 April ± 13 days (Table1). Onset of breeding started on 25 April ± 13 days (Table 1).

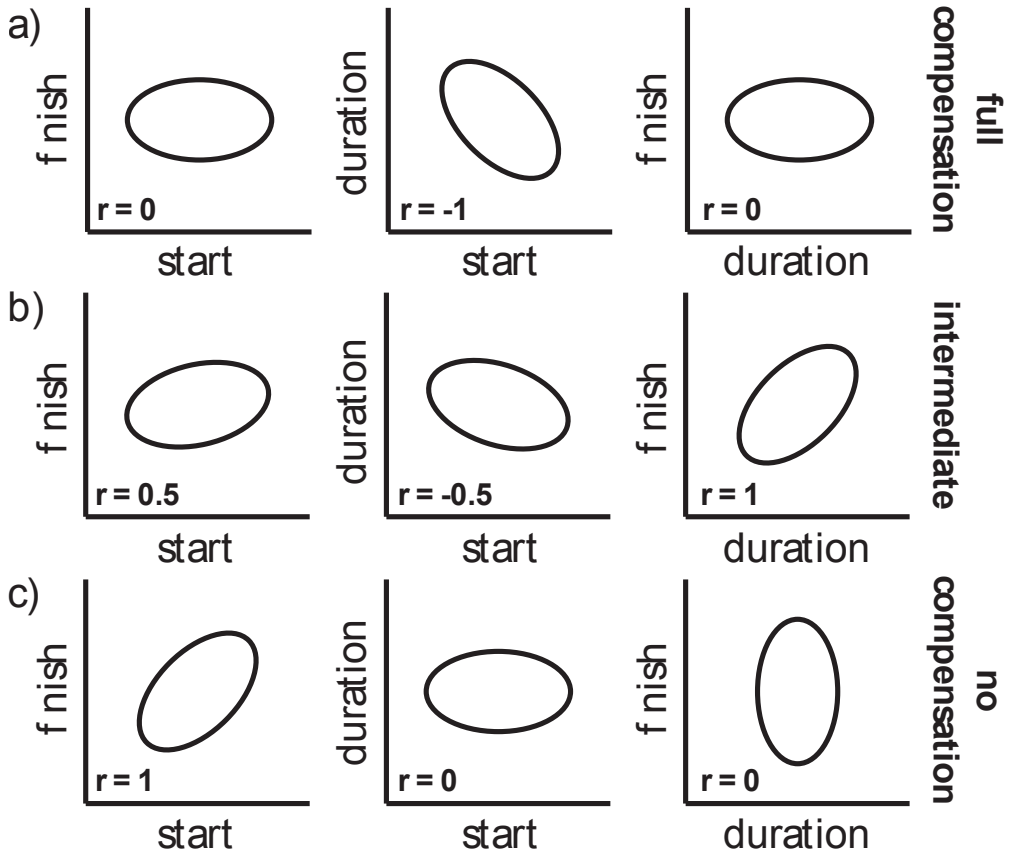

Figure 2. Schematic overview of compensation scenarios. Under full compensation (a), the duration of a period would be variable with a fixed finishing date. If there was no compensation (c) duration of a period would be fixed, but the start and/or finish would be variable. Between these two extremes; the duration, start and finish of a period would be variable to some extent under an intermediate compensation (b).

Table 1. Overview of the timing of key events in male and female adult Hoopoes, characterized by median date or duration (days), interquartile range (in parentheses) and number of individuals (N).

event	males	females
fledging date	14 July (39, N=29)	11 July (28, N=28)
departure date from breeding	18 August (13, N=29)	15 August (16, N=27)
duration of post-fledging period	32 (25.5, N=27)	37 (31, N=27)
arrival date in wintering	23 September (14, N=23)	25 September (18, N=28)
autumn migration duration	34 (18, N=27)	35 (21, N=27)
departure date from wintering	10 March (14, N=24)	10 March (14, N=26)
duration wintering	167 (24, N=28)	163 (31, N=28)
arrival date in breeding	6 April (10, N=23)	4 April (11, N=25)
spring migration duration	22 (13, N=24)	26 (19, N=25)
onset date of breeding	24 April (10, N=24)	27 April (14, N=25)
duration of pre-laying period	17 (14, N=16)	21 (22, N=24)
duration of breeding season	58 (42, N=28)	78 (43, N=28)

Sequential dependence of timing

Departure from the breeding grounds strongly depended on the end of the breeding season (Table 2A). The top three models for the departure from the breeding grounds furthermore included either the number of broods or the number of fledglings, but their effects were weak and no year effects were found (Table 2A). Arrival in the wintering grounds also strongly depended on the timing of the previous event; departure from the breeding grounds (Table 2B). The top models on the arrival in the wintering grounds furthermore included sex, the duration of the post-fledging period, autumn migration route or year (Table 2B). Again, effects were weak, except for the effect of the autumn migration route. Most birds migrated via islands in the Western Mediterranean Sea (N = 25) and arrived 1-2 days earlier in the wintering grounds than birds that migrated via the Iberian Peninsula (N = 18) and roughly one week earlier than birds that migrated via mainland Italy (N = 11; Table 2B).

Departure from the wintering grounds was mainly determined by the duration of stay in the wintering grounds rather than arrival in the wintering grounds, and, to a lesser extent, by sex or year (Table 2C): birds that stayed longer in winter, departed later and females departed slightly later than males (Table 2C). Finally, arrival in the breeding grounds was more determined by the duration of spring migration rather than solely by the date of departure from the wintering grounds. Birds that took longer for spring migration, arrived later in the breeding grounds (Fig. 5A and Table 2D). The three top models furthermore included sex or nestbox occupancy, but effects were weak (Table 2D).

Variability in timing

Individuals varied greatly in the timing of periods and the variability significantly decreased towards the breeding grounds, and increased again for the timing of the onset of breeding (Fig. 3, $P < 0.001$, Bartlett test).

Compensation

Adults compensated for all timing events to some degree (Fig. 4), yet the degree of compensation varied: Compensation was strongest for birds that arrived late in the wintering grounds: they compensated with a shorter wintering period (Fig. 4c). Some compensation was possible during autumn migration (Fig. 4b), which was in contrast with spring migration where birds hardly compensated - birds that departed late from the wintering grounds arrived later in the breeding grounds (Fig. 4d).

Finally, in general hoopoes that arrived later, started breeding later (Fig. 4e and Table 2E), but this could be partially compensated for by shortening the pre-laying period (Figure 4e).

Table 2. Overview of effect sizes (±SE) of explanatory variables included in the best three models for the timing of events in adults. For an overview of all tested models see Appendix 2. The intercepts correspond to males and a migration route via the Iberian Peninsula.

A: departure from the breeding grounds

intercept	fledging date	#broods	#fledglings	Akaike weight
175.89 (12.67)	0.27 (0.07)			0.17
170.07 (13.19)	0.34 (0.08)	-4.02 (2.81)		0.15
175.19 (12.59)	0.30 (0.07)		-0.64 (0.47)	0.14

B: arrival in the wintering grounds

Intercept	departure breeding	post-fledging period	direction autumn migration[1]	sex	year	distance[2]	Akaike weight
181.15 (32.70)	0.40 (0.14)	-0.17 (0.10)					0.15
213.31 (45.99)	0.27 (0.16)		-2.00 (4.60) – 7.82 (5.48)	1.90 (3.87)	x	-0.00 (0.01)	0.12
179.17 (33.31)	0.38 (0.15)						0.10

C: departure from the wintering grounds

Intercept	duration wintering	year	Sex	Akaike weight
25.58 (14.23)	0.26 (0.08)			0.67
24.19 (14.86)	0.26 (0.09)		1.01 (2.76)	0.22
14.87 (16.27)	0.33 (0.10)	x		0.05

D: arrival in the breeding grounds

Intercept	duration spring migration	nestbox occupancy	sex	Akaike weight
82.92 (2.87)	0.45 (0.11)			0.55
84.46 (4.18)	0.45 (0.11)	-0.02 (0.04)		0.19
82.53 (3.12)	0.45 (0.11)		0.76 (2.19)	0.18

E: onset of breeding

Intercept	duration spring migration	pre-laying period	nestbox occupancy	sex	Akaike weight
101.53 (6.33)	0.36 (0.11)	0.66 (0.11)	-0.12 (0.05)		0.57
102.31 (6.39)	0.36 (0.11)	0.68 (0.12)	-0.12 (0.05)	-2.26 (2.65)	0.23
91.05 (4.66)	0.40 (0.11)	0.72 (0.12)			0.12

F: number of fledglings in the first brood

intercept	nestbox occupancy	arrival breeding grounds	sex	onset of breeding	Akaike weight
-1.22 (2.83)	0.03 (0.01)	0.04 (0.03)			0.14
2.50 (3.47)	0.02 (0.01)	0.05 (0.03)	-0.88 (0.56)	-0.03 (0.03)	0.12
1.71 (3.49)	0.02 (0.01)	0.06 (0.03)		-0.04 (0.03)	0.12

G: total number of fledglings

intercept	onset of breeding	duration spring migration	nestbox occupancy	arrival breeding grounds	Akaike weight
17.02 (3.99)	-0.16 (0.03)			0.09 (0.04)	0.34
14.16 (4.86)	-0.14 (0.04)		0.02 (0.02)	0.09 (0.04)	0.17
16.41 (4.14)	-0.16 (0.04)	-0.02 (0.04)		0.10 (0.05)	0.12

1) effect sizes in the left column indicate difference of taking a route via islands in the Mediterranean Sea between the Iberian Peninsula and Italy, the right column indicates the difference for a route via mainland Italy

2) great circle distance from the breeding to the wintering grounds in km

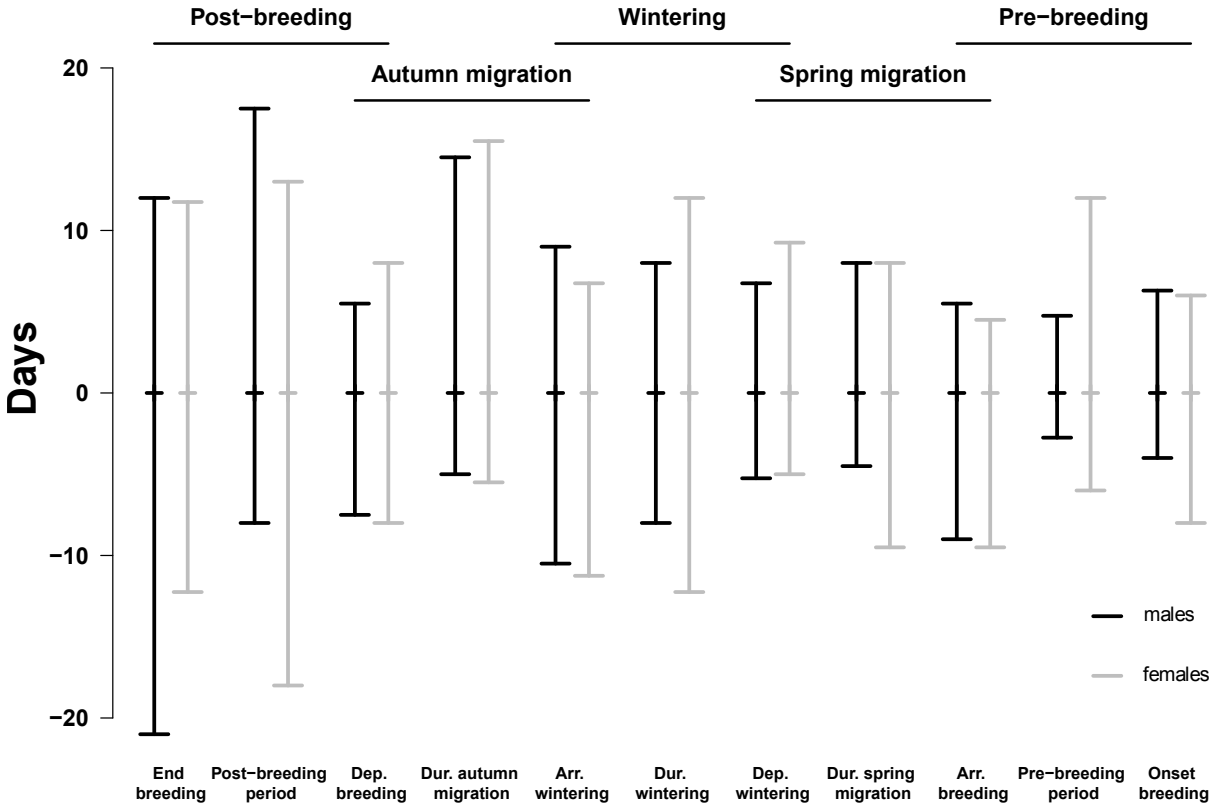

Figure 3. The variability in the timing of events and the durations of periods throughout the annual cycle. The median is standardized to 0, the whiskers indicate the 1st and 3rd quartile.

Relationship between arrival, onset of breeding and reproductive success

The onset of breeding was delayed with a longer spring migration, longer pre-laying period and delayed birds occupied lower quality nestboxes (Table 2E).

The number of fledglings in the first brood was mainly determined by the quality of nestboxes: better territories produced more fledglings (Table 2F and Fig. 5a), and it was also weakly influenced by arrival in the breeding grounds, onset of breeding and sex (Table 2F).

The total reproductive output declined with a later onset of breeding (Table 2G and Fig. 5b). The best three models also included the duration of spring migration, nestbox occupancy and date of arrival in the breeding grounds, but effects were weak (Table 2G).

Discussion

The timing of events depended on the timing of the previous event throughout the annual cycle, and the variability between individuals in timing decreased towards the breeding grounds. Similarly, there were also important differences in the potential for compensation, which was largest during the post-breeding and wintering period, but virtually absent during the pre-breeding period.

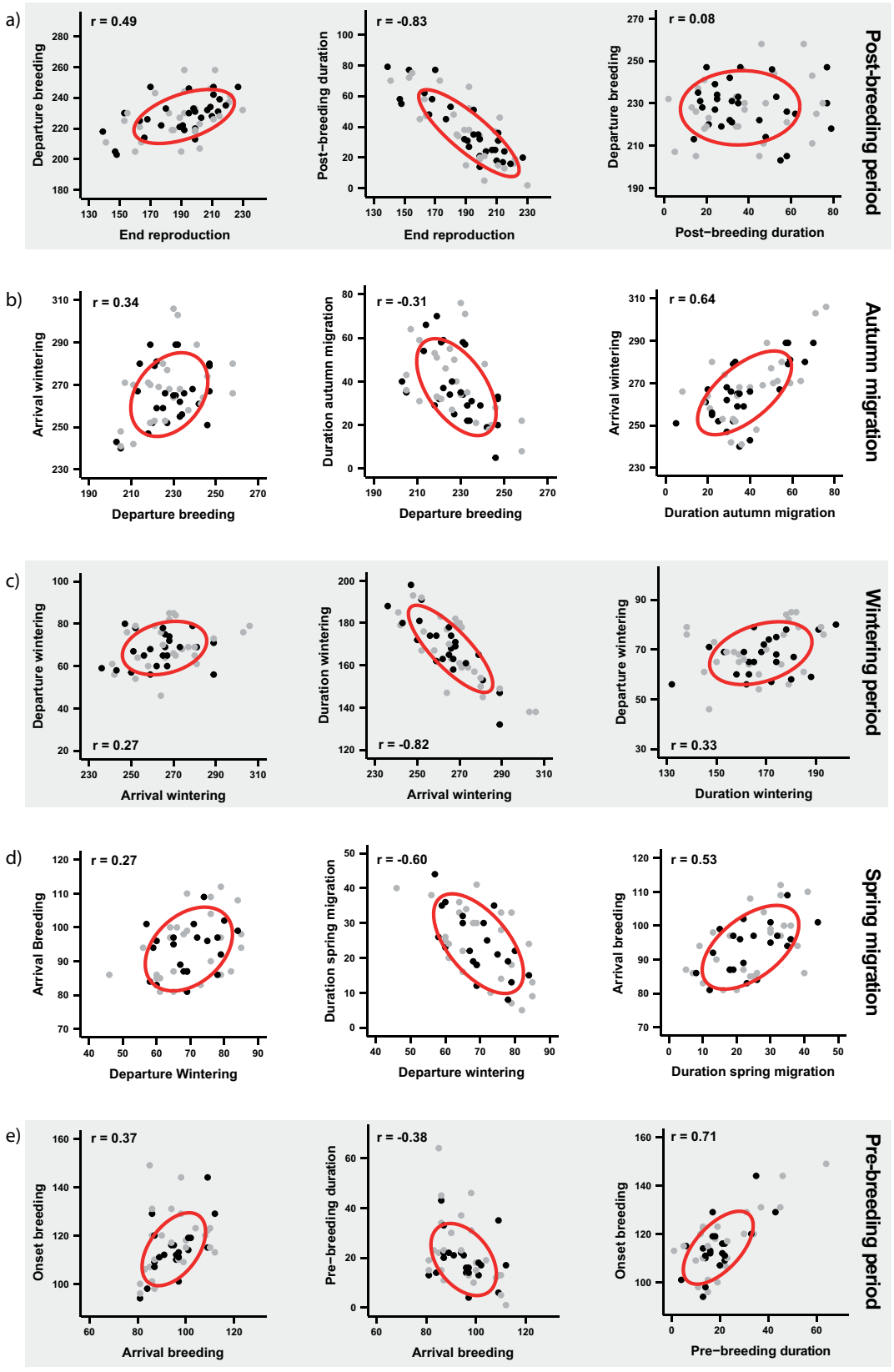

Figure 4. Dependencies between start, duration and finish of various periods for comparison with patterns expected under the three scenarios in Fig. 2. Black circles represent males, grey circles females and the ellipses encompass 70% of the data, indicated are the average Person's correlation coefficient.

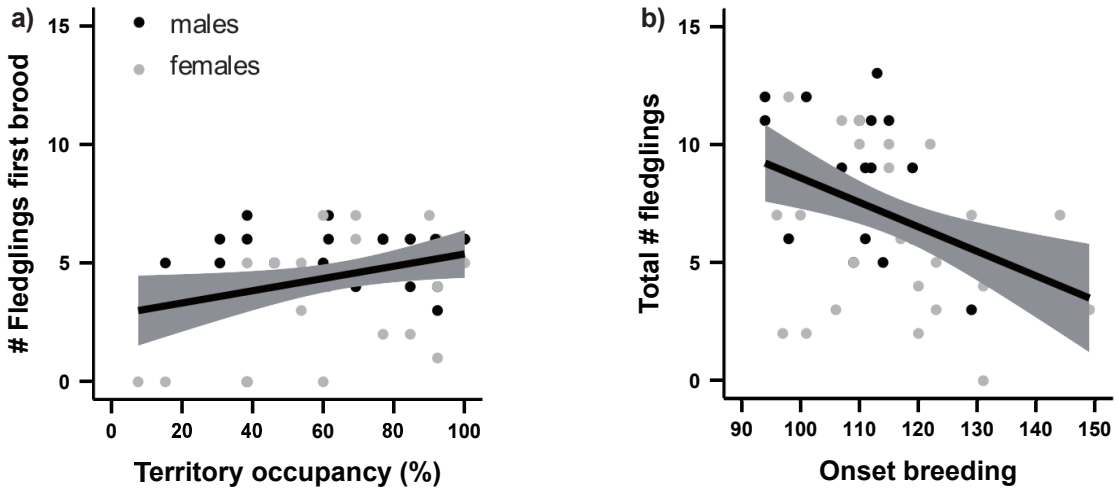

Figure 5. The relation between A) nestbox occupancy and the number of fledglings in the first brood and B) the onset of breeding and the total reproductive output in adults.

Furthermore, we could show that timing had fitness-consequences: birds that arrived later in the breeding grounds started breeding later and had lower reproductive success.

Dependencies between timing events weakened towards the end of the wintering period. The wintering period thus functioned as a reset in timing dependencies, where birds could compensate for previous mistiming supporting earlier findings in ducks and shorebirds (Oppel et al. 2008, Senner et al. 2014). It implies that up to the wintering period, arriving or departing late can be counteracted at least to a certain extent. As many passerines moult in the wintering grounds, this might be achieved, e.g. by increasing moult rates (Helm et al. 2005, Barta et al. 2008, Morrison et al. 2015). Before the wintering period, birds could compensate during the post-breeding period by decreasing the post-breeding duration or, interestingly, by adopting a faster migration route in autumn. Indeed, most Hoopoes migrated along the fastest route via islands in the Western Mediterranean Sea and saved up to a week compared to a route via mainland Italy.

Compared to autumn migration and the duration of the wintering period, the timing of spring migration was hardly variable between individuals, probably since there is strong selective pressure to arrive on time in the breeding grounds (Kokko 1999, Vardanis et al. 2011, Gienapp and Bregnballe 2012, Tøttrup et al. 2012, Nilsson et al. 2013) Although the specific cues that initiate departure from the wintering grounds have yet to be determined, the low variability in timing between individuals indicates the existence of an universal cue, e.g. photoperiod (Berthold 1996). The variability

between individuals could be related to different sensitivity to this cue (Coppack and Pulido 2009) or to differences in the quality of wintering sites that influence the time required to prepare for spring migration. Birds might be able to compensate a late departure from the wintering grounds by increasing flight speeds (Fransson 1995, Coppack and Both 2003, Klaassen et al. 2008, López-López et al. 2010) or by reducing the time spent on stopovers (Weber and Hedenström 2000, McLaren et al. 2013, Smith and McWilliams 2014). But there will be a limit after which this will bear costs, since birds might need more time to recover from migration after arrival. After arrival birds will have to get prepared as soon as possible for breeding and decide based on the local environmental conditions whether to start breeding straight away or wait for conditions to improve (Gienapp and Visser 2006, Legagneux et al. 2012). But when this period is too short, it will likely also come at a cost. Especially so for females that have to acquire enough resources for egg laying, that most likely in (near)passerines are taken up in the breeding grounds (Langin et al. 2006).

Finally, we found that total reproductive success was mainly affected by the date of arrival and onset of breeding, but the reproductive success of the first brood was mainly influenced by the duration of spring migration. The survival of young however differs over the course of the breeding season: Young produced early in the season are more likely to return in the subsequent year compared to young of later broods (Hoffmann et al. 2015) and therefore, fledglings of early broods yield a higher fitness-payoff than fledglings from late broods. Selection pressure will thus favour a short spring migration and an early arrival. Yet, Arriving too early can also incur a penalty, especially in breeding locations at more northern latitudes where weather conditions at the beginning of the season still can be harsh (Bêty et al. 2004, Tøttrup et al. 2010).

We conclude that understanding the temporal constraints within the annual cycle and defining sensitive periods, i.e. those with few potential for compensation, is crucial to understand the population dynamics of migrating species, but also is of great importance for a proper, effective conservation.

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CHAPTER 7 – IDENTIFYING DRIVERS OF BREEDING SUCCESS IN A LONG-DISTANCE MIGRANT BIRD USING STRUCTURAL EQUATION MODELING

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Abstract

In migrant animals, conditions encountered during the non-breeding season and on migration may affect subsequent breeding success. Yet, most studies so far have investigated the effect of specific parts of the annual cycle only, most often the non-breeding season or spring migration. However, thereby it is omitted how these events can interact throughout the annual cycle and how individual quality plays a role to explain breeding success.

We estimated the effects of both the previous breeding season and the migration cycle on breeding success in Hoopoes (*Upupa epops*) using a structural equation approach. Our causal framework explained 75% of the variation in breeding success. The direct effect of the previous breeding attempt had the highest effect and positively impacted breeding success. The effect of the migration schedule was negligible.

Our results suggest that the interplay of individual quality and conditions during both the previous and current breeding season may be more important drivers of breeding success than solely the schedule of migration, even in a long-distance migrant bird as the Hoopoe. Further analysis integrating more information about weather and climate during migration and the breeding season are however needed to provide a wider overview of the annual life cycle of Hoopoes and disentangle the (in)existence of carry-over effects from migration onto breeding success.

Keywords: carry-over effects, hoopoe, geolocator, intrinsic quality, annual cycle

Introduction

Carry-over effects (COEs) occur when processes or events in one season influence the success of an individual in the following season and are common in several taxa, from mammals to invertebrates (Festa-Bianchet 1998, Harrison et al. 2011, Ceriani et al. 2015). They are especially frequent in migrant species (Betini et al. 2014, Clausen et al. 2015, Cooper et al. 2015) as long-distance journeys incur costs (Newton 2008). Physiological depletion, weather conditions during the journey itself and on the non-breeding site, and food availability can all result in COEs and finally affect fitness (Alerstam et al. 2003, Newton 2008). Environmental conditions in the non-breeding site and the timing of spring migration have most commonly been investigated to explain current reproductive success in COE studies, however, the links between all events in an annual cycle are often ignored. Recently, Marra et al. (2015) expressed the need for an holistic approach focusing on all seasons within a year to improve our understanding of movement ecology.

Several major challenges exist when investigating COEs. First, year-round data are needed, i.e. on breeding performance, migratory behaviour, location of the non-breeding site and environmental conditions at all places visited, which requires tracking of individuals throughout the year (Harrison et al. 2011). Second, it is often difficult to disentangle the effect of intrinsic and external factors and processes (Daunt et al. 2014). For instance, environmental conditions in the non-breeding sites may influence individual (body-)condition prior to pre-breeding migration (Sedinger et al. 1990, Norris 2005), which can impact the timing of spring migration and thus breeding success (Low et al. 2015). Another critical challenge is to analyse the different events and process within the same framework. A powerful and promising approach in ecology is the use of structural equation models (SE models) (Grace et al. 2010) - probabilistic models that evaluate multiple causal pathways and include both direct and indirect effects (Grace 2006). SE models use latent variables, i.e. conceptual variables that are constructed by one or more observed variable(s), and thus account for the measurement process (Grace 2006).

SE models appear an ideal approach to investigate COEs as they offer the possibility to estimate the relationship between several latent variables and breeding success. The effect of previous on current breeding performance can occur through intrinsic individual quality (McCleery et al. 2008) or by a series of COEs triggered by events on the journeys from and back to the breeding grounds and non-breeding sites (Shoji et al. 2015). Modelling both the direct relationship of previous breeding success on current breeding success and the direct relationships of non-breeding periods on breeding success in SE models allows to clearly distinguish the effect of intrinsic quality from COEs on breeding success and to assess their relative importance.

In the present study, we investigate COEs during the annual cycle in a long-distance migrant - the Hoopoe *Upupa epops,* in Switzerland. We reconstructed the annual cycle of more than 50 individuals between subsequent breeding bouts from geolocator data, characterising breeding outcomes, timing of migration (both movements in autumn and spring) and location of wintering (non-breeding) sites. Using SE models, we evaluated the relationship between each step of the annual cycle and breeding success, and thus quantified in how far breeding success was shaped by previous breeding performance, autumn migration, time spent and conditions encountered on the wintering grounds and finally spring migration.

Material & Methods

(a) Model species

We investigated a population of Hoopoes breeding in south-western Switzerland (46°14'N 7°22'E), a study area of about 62 km^2 with ~550 nest boxes (Arlettaz et al. 2010). Hoopoes are terrestrial feeders, relying on large soil invertebrates, and they are long-distance Palaearctic-African migrants, which spend the wintering season in the Sahelian belt south of the Sahara (Bächler et al. 2010). Birds typically return to the breeding grounds in early April, start breeding in late April, and the last nestlings fledge in early August (Hoffmann et al. 2015). Most hoopoes in our study population produce one clutch per year, but one third has two or more clutches (Hoffmann et al. 2015).

(b) Data collection

Hoopoes were caught in or at nest boxes and marked with a unique combination of one metal and three colour rings. Additionally, we equipped a random subsample of individuals with geolocators of type SOI-GDL1 (see Bächler et al. 2010 for a complete description of the device). The tracking devices had no effects on reproduction, condition and survival in hoopoes (van Wijk et al. 2015). From 2008 to 2013, 328 breeding hoopoes were equipped with geolocators, of which 54 were retrieved in the following year (see Appendix Table A1 for a breakdown by sex and year). For these birds, we determined timing of migration, location of wintering areas and breeding performance (number of clutches and the number of fledglings of the first clutch).

(i) Characterisation of Migration

Based on geolocator data, we determined individual migration schedules and location of wintering areas (Schmaljohann et al. 2015, van Wijk et al. *in prep* for details). Migration schedules were characterised by timing, i.e. start and duration of autumn and spring migration. We used the

normalized difference vegetation index (NDVI) to characterise conditions in wintering areas as these correlate with physical conditions (temperature and rainfall) and thus, probably food availability (e.g. Clausen et al. 2015). We retrieved NDVI values from U.S Geological Survey Famine Early Warning System network (FEWS NET http://earlywarning.usgs.gov/fews/index.php) and used the median NDVI values over the months October to February as a proxy of general conditions and the difference between median NDVI values in October and February ($\Delta NDVI = NDVI_{Feb} - NDVI_{Oct}$) as an index of the variation over winter.

(ii) Breeding performance

At the breeding grounds in Switzerland, nestboxes were surveyed every two weeks from the beginning of the breeding season. Occupied nestboxes were subsequently visited every three days to obtain the number of eggs, hatchlings and fledglings, and the timing of incubation, hatching and fledging. For each individual, we recorded the number of clutches and the number of fledglings.

(c) Investigating causal relationship using structural equation model

(i) Causal framework

Structural equation models typically combine a measurement model that defines latent variables from one or more observed variables with a structural regression model that links these latent variables (Grace 2006). This latter model can then test assumptions on causal relations between latent variables depending on the link between them.

We aimed at explaining breeding success in the hoopoe population assuming causal relationships between the following latent variables: previous breeding success, timing of autumn and spring migration and of the wintering period, location and conditions of the wintering grounds and current breeding success, following the approach described by Grace et al. (2012). Current breeding success was thus the dependent latent variable in our model while all others were independent latent variables. We defined all latent variables from the following measured variables: a) previous breeding success (PB) from the number of fledglings in the first brood of the previous year and the number of broods in the previous year; b) autumn migration (AU) from the departure date from the breeding grounds and the duration of autumn migration; c) wintering timing (WiT) from arrival and departure dates from the wintering ground; d) winter conditions (WiC) from median NDVI and ΔNDVI; e) spring migration (SP) from departure from the wintering grounds and the duration of

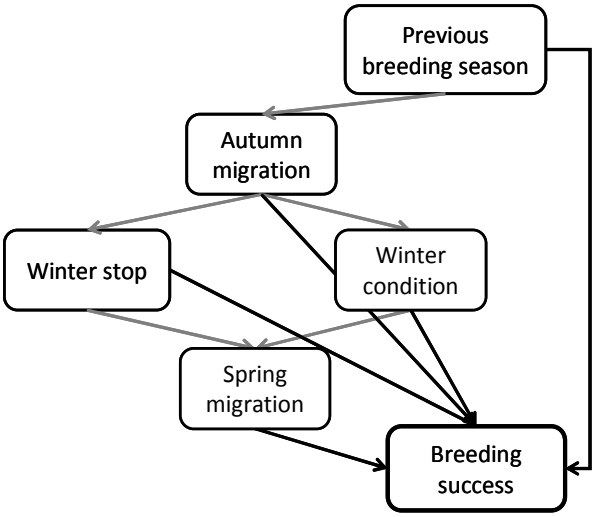

Figure 1. Conceptual diagram of how variables were linked to each other. Directional arrows refer to the direction of the causal relationship. Grey and black arrows represent respectively indirect and direct effects of variables on the breeding success.

spring migration, and f) current breeding success (BS) from the number of fledglings in the first brood and the number of broods in the current year.

Our causal framework followed a chronological pathway (Fig.1) and assumed that the previous breeding success could directly affect current breeding success (black arrows on Fig.1), that autumn and spring migration, wintering timing and wintering conditions could have direct effects on breeding success and that due to timing constraints, autumn migration could have an effect on winter timing and conditions, and both could in turn have an effect on spring migration. Thus, the model not only tested direct influences on current breeding success but also potential indirect effects, e.g. previous breeding success via autumn migration, wintering and spring migration (grey arrows on Fig.1).

(ii) Implementation of our structural equation model

Following the notation from Grace (2006), the measurement model is:

$$x_{ij} = \lambda_i \xi_j + \delta_j$$

$$y_{ik} = \lambda_i' \eta_k + \varepsilon_k$$

Where x_{ij} and y_{ik} are measured variables associated to independent latent variable *j* and dependent latent variable *k*, respectively, λ_i and λ_i' are the loading factors linking the measured variable *i* to an independent and dependent latent variable, respectively, ξ_j is the latent independent variable *j*, η_k the dependent latent variable *k*, and δ_j and ε_k are measurement and residual errors, respectively.

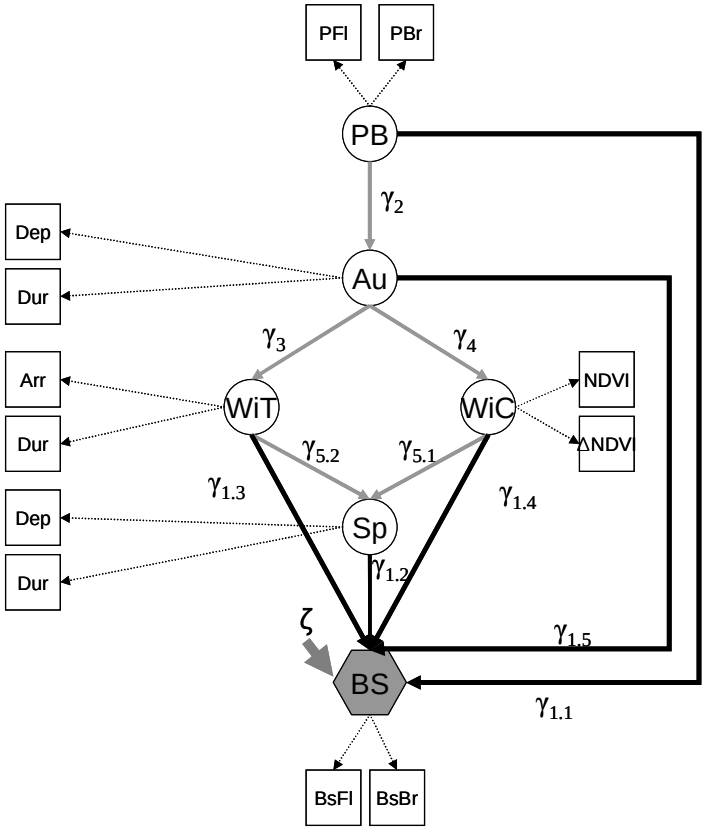

Figure 2. Conceptual diagram with all measured variables for each latent variable. Circles and rhombus represent independent and dependent latent variables, respectively. Squares are measured variables. Arr = arrival date; Dep = departure date; Dur = duration of the migration; End = end of the breeding season; NDVI = median value of NDVI over the wintering period (from October to February); ΔNDVI = difference between February and October values of NDVI; #Br = number of broods for each individual in Previous (PBr) or current breeding season (BsBr); #Fl = number of fledglings raised in first brood in Previous (PFl) or current breeding season (BsFl); PB = previous breeding attempt, AU = autumn migration, WiT = winter timing, WiC = winter condition, SP = spring migration, BS = breeding success. Grey and dark arrows represent indirect and direct effects, respectively, of latent variables on breeding success with associated parameters. ζ refers to the residual variance of the latent breeding success variable.

Our structural model (Fig.2) is: $\eta_k = \gamma_{kj}\xi_j + \zeta_k$

With γ_{kj} being the structural coefficient describing the effect of the independent latent variable ξ_j on the dependent latent variable η_k and ζ_k the residual variance.

Due to the relatively restricted sample size (54 individuals) and presence of both categorical and continuous variables in the dataset, we estimated the parameters of the measurement and structural model using Markov Chain Monte Carlo (MCMC) simulations in the Bayesian framework.

This is a robust method even with low sample sizes (Grace et al. 2012). We specified non-informative prior distributions for all parameters to be estimated (see R script given in Appendix B for a complete specification of the model and priors used). The model was implemented using the program WinBUGS (Lunn et al. in press) called from R (R Core Team 2014) with package R2WinBUGS (Sturtz et al. 2005).

Since we wanted to compare their relative influence, we standardized the independent variables and thus, all estimated coefficients are standardized and quantify the relative change in the dependent variable with changes in the independent latent variable(s). The total effect of a latent variable is the sum of both direct and indirect effects (black and grey arrows in Fig. 1). The total explained variance of breeding success R^2 can be derived easily from the unexplained variance of breeding success (ζ) as $R^2 = 1 - \zeta$ (Grace 2006). A Bayesian p-value was computed to assess the fit of the model to the data where values close to 0 or 1 are suspicious (Kéry and Schaub 2012).

Results

Our structural equation model seemed to fit the data generally well (Bayesian p-value = 0.49) and explained around 75% of the variance in current breeding success (1- ζ, Fig 3).

Previous breeding had a direct positive influence on the current breeding success ($\gamma_{1.1}$=0.69, 95% Credibility Interval [0.40;1.06], Table 1) but its indirect effect through the migration pathway (i.e. the product of coefficients) was equal to 0. Autumn migration had a slightly positive effect on winter timing (γ_3=1.56) but only a weak effect on winter conditions (γ_4=0.51). Winter timing and winter conditions had nearly no effect on spring migration (-0.17 and 0.12, respectively). Finally, spring migration had nearly no influence on breeding success ($\gamma_{1.2}$=0.02)

Discussion

Using a structural equation model, we evaluated the effect of the previous breeding success and each step of the migration cycle on current breeding success. Unexpectedly, none of the migration stages was found to influence current breeding success suggesting the absence of carry-over effects. However, we found a direct positive relationship between previous and current breeding success, suggesting strong intrinsic effects.

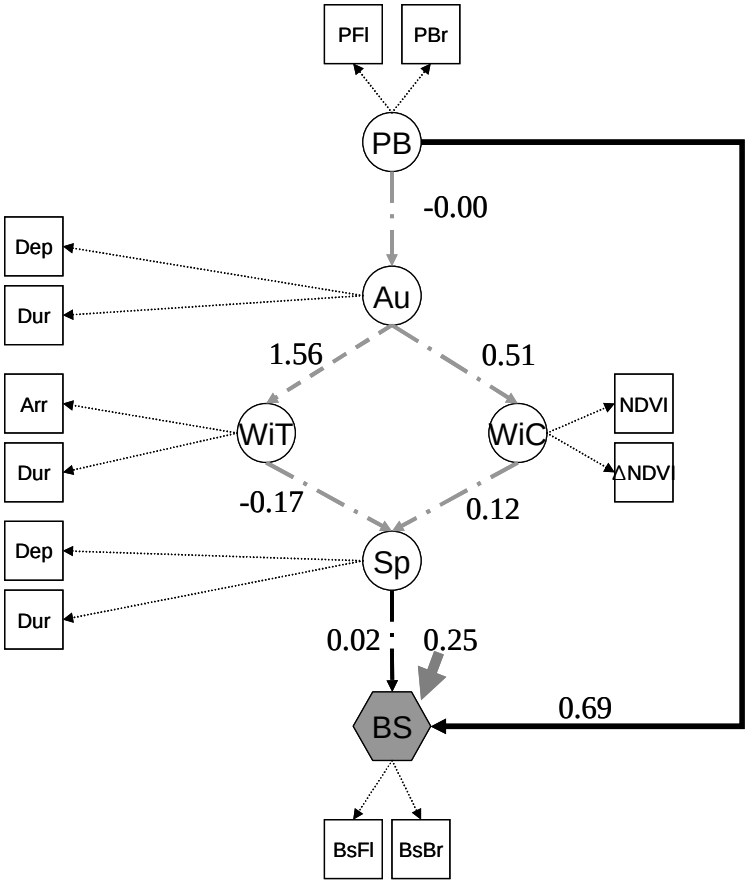

Figure 3. Final structural equation model for the annual cycle of hoopoes with standardized estimates of path coefficients.

(a) No relationship between successive stages

A striking result of our analysis was the absence of a relationship between stages of the migration cycle. The annual cycle of migratory birds is thought to be time-constrained and we expected strong relationships both between consecutive steps of the migration cycle (Newton 2008) and especially between spring migration timing and breeding success, which has been found to be highly correlated in several studies (Bêty et al. 2004, Tryjanowski et al. 2004, Catry et al. 2013, Low et al. 2015).

One explanation for the weak link between successive steps of the non-breeding life cycle may be due to absence of COEs inside the migration cycle (Ockendon et al. 2013, Senner et al. 2014). Deviation from the average behaviour in one season may not persist until the next season when animals can compensate (Conklin and Battley 2012, Conklin et al. 2013). For example, individuals that arrive late on wintering grounds may increase foraging effort or moulting rates to catch up and start spring migration at a similar time like early-arriving individuals. Such compensation may also explain the weak link between spring migration and breeding success found in our analysis (Senner et al. 2014): birds arriving later on the breeding grounds may shorten the pre-laying period and

eventually achieve a similar breeding performance like birds that arrived earlier. This is probably the case in hoopoes where van Wijk et al. (*in prep.*) found only weak effect of the arrival date on the breeding ground on the number of fledglings in the first brood or on the total number of fledglings. Furthermore, variability in arrival dates on the breeding ground was smaller than one of the other timing events, suggesting the existence of an arrival time window allowing all individuals that arrive in this window to achieve similar reproductive success.

However, there are also methodological issues that may explain the absence of a relationship between stages. In our structural equation approach, we did not test the effect of one observed variable to another one. Instead, we defined a latent migration variable combining departure date and the duration of migration. We also accounted for residual variance in the latent variable to take into account other sources of variation. Our results suggest that this residual variance may be equally or more important than variance explained by the timing component (departure and duration), leading to weak estimates of the relationship between latent variables. Phenomena such as conditions encountered during migration (e.g. weather or wind conditions (Liechti 2006), length of migration routes or the number of stop-overs (Arlt et al. 2015) may be responsible for this high residual variance. Further integration of such processes into latent variables may clarify the relationship between successive stages in an annual cycle analysis.

(b) Carry-over effect on breeding success?

We found a strong positive link between successive breeding attempts, yet links between steps of the non-breeding season and breeding success were very weak. This suggests that there are no COEs on breeding success but that it is mainly driven by previous breeding success.

Although the absence of COEs might be surprising at first, it has been found in several species when considering the full annual cycle (Ockendon et al. 2013, Senner et al. 2014). One explanation would be the compensation hypothesis (Clausen et al. 2015): individuals might be able to compensate for 'mistiming' (i. e. deviations from some optimal time) or, alternatively, penalties for mistiming might not be strong – both of which could leading to the absence of effects on their breeding success (Conklin and Battley 2012).

Another explanation might be the great relative importance of the previous breeding season on breeding success. Irrespective of events and processes during the non-breeding season, their effect on breeding success might be masked by the (dominating) effect of the previous breeding season, conditions during the current breeding season or individual quality (Ockendon et al. 2013).

This relationship can likely be explained by individual quality being the major driver of breeding success. Hoffmann et al. (2015) showed that the number of fledglings in the first clutch was an important factor associated with double-brooding and that intrinsic quality (e.g. ability to occupy a higher quality territory) was a driver of double-brooding. Individuals of high quality were able to raise a high number of fledglings at the first brood and to make a second clutch (Hoffmann et al. 2015). Breeding success is also related to territory quality and early broods are initiated in high quality territories suggesting that early arriving individuals occupy the best territories (Tschumi et al. 2014).

Conditions during the breeding season may also explain the link between past and current breeding outcomes (Ockendon et al. 2013). Previous studies have shown that reproductive output in Hoopoes is influenced by weather and climate (Martín-Vivaldi et al. 1999, Arlettaz et al. 2010), with rain and low temperature being unfavourable while higher temperatures positively influenced reproductive success. Spring conditions in the breeding grounds were quite variable over the last 5 years (van Wijk *unpublished data*). However, breeding performances in two consecutive years remained positively related over time suggesting that some process occurred to mitigate the effect of weather, such as positive carry-over effects. For instance, lower investment in one year, either due to early failure or good weather conditions may allow for a better recovery after breeding, which may in turn enhance the breeding success in the subsequent year (Catry et al. 2013, Shoji et al. 2015).

(c) Structural equation model as a tool to investigate the annual cycle

To investigate COEs in the annual cycle of hoopoes, we used the structural equation modelling approach rather than classical methods such as generalized linear models or path analysis. We created a causal framework embracing the full annual cycle of a long-distance migrant and separated the effect of individual quality from the effects of migration journeys and non-breeding periods. Thus, this structural equation model provided a novel tool for testing various assumptions underlying the causal framework and for estimating the relative importance of potential drivers of breeding success. Such models allow to integrate measurement error and residual variance and thus, provide a more general, comprehensive view of the entire process. When set up within a Bayesian framework, SE models deliver reliable results even for low sample sizes (Grace et al. 2012), thanks to prior information given in the model and Markov Chain Monte-Carlo estimation processes.

The low sample size did not permit to do a selection for the causal framework. For example, instead of using a chronological pathway from one breeding season to the subsequent one, one may decide to build an alternative pathway not following the annual cycle with other conceptual

variables (1 for all departure dates irrespective of the migration step, one about length of migration steps, another one about wintering conditions, etc.). Another structure may present a different perspective to supplement our current findings.

Overall, structural equation models are a novel and promising tool to investigate causal relationships such as carry-over effects and to improve our understanding of complex mechanisms such as migration in ecology.

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CHAPTER 8 – GENERAL DISCUSSION

The study of migrating birds has thrived in recent years with the development of newer, lighter, intelligent tracking devices, especially so called geolocators. The wealth of new data that their applications yielded generated many new insights and made it possible to conduct this PhD thesis. In this thesis, I described migration patterns of Hoopoes and Wrynecks and investigated, among others, the potential for compensation during the annual cycle, individual repeatability of migratory behaviour and consequences of migration timing on reproductive success in Hoopoes. Also I studied whether carrying a geolocator might negatively impact an individual's physical and physiological state or alter the annual apparent survival.

Carrying a device might have several impacts on the individual, all of which could alter its (migratory) behaviour. This has the consequence that behaviour is recorded that is no longer representative for the study population, thus compromising inference. Although several earlier studies have found some effects on equipped individuals (see Barron, Brawn, & Weatherhead, 2010; Costantini & Møller, 2013 for examples), these studies often were based on low sample sizes and a limited set of response variables. Furthermore, survival in these studies was typically defined by return rates, even though these are often confounded by other factors, e.g. observation probability.

I investigated effects of geolocators in Hoopoes on a range of traits over multiple years with an extensive sample size and included a capture-recapture model to estimate apparent annual survival in equipped and control birds. Geolocator and control birds did not differ in any of the traits investigated when data were pooled for all years, but there were slight – mostly positive – geolocator effects in individual years. The results of this chapter emphasize that studies on effects of tagging devices require: i) an ample sample size to draw valid conclusions, ii) a study over multiple years: selecting solely one or two years might result in wrong inference, since the environment could have an additive effect on top of carrying a device in certain years, iii) a proper design of the device and a minimization of the relative weight for as much as possible and iv) the use of a capture-recapture model for the estimation of apparent annual survival, since this is more reliable and objective compared to solely relying on return rates.

For surprisingly many migrating birds it is still unknown where exactly they winter and across which routes they get there. Tracking devices can yield a wealth of information and scrutinize long-held beliefs about the whereabouts of migratory birds outside the breeding season, i.e. where they spend significant proportions of their lives (Mckinnon et al. 2013). There are numerous recent examples for these, e.g. instead of presumed wintering sites in Sahelian Africa, birds have turned up

in the Middle East or India (Hedenström et al. 2013) and instead of being bound to coastal ecosystems, some waders winter in the Sahel region (Lislevand and Hahn 2015). One example for such a revision about the location of wintering areas resulted from the application of geolocators to Wrynecks (Chapter 3). Here, I described that contrary to earlier believes, Eurasian Wrynecks from Central European populations winter on the Iberian Peninsula and in Northern Africa. This finding is not only of scientific interest, but also highly relevant for a successful conservation, since management measures would need to be installed in other locations than previously suspected.

That Wrynecks of our study population winter in relatively easy to locate areas gave the opportunity to study finer-scale occurrence and habitat use mid-winter *in situ*. I investigated the occurrence of Wrynecks in the northern Extremadura, Spain. The selection of this region was based on the geolocator findings and the wintering atlas of Spain (SEO/BirdLife 2012). Wrynecks were indeed found in the northern Extremadura and in very specific habitat: they avoided the most frequently occurring habitat type - dehesas - and birds seemed to congregate in extensive agricultural landscapes with a mixture of olive or fruit orchards, irrigated cropland and shrubs. Thus, Wrynecks appear to be very dependent on specific agricultural landscapes throughout their annual cycle, which might be a peril when these landscapes decline in the course of fundamental agricultural changes.

On an individual level it might be an advantage to adopt a flexible migration strategy; changing routes, timing and wintering sites between years. However, many studies have found individual timing and wintering sites to be highly repeatable between years (Vardanis et al. 2011; Stanley et al. 2012; López-López et al. 2014; Senner et al. 2014; Yamamoto et al. 2014; Blackburn and Cresswell 2015). In contrast to these findings, I show that Hoopoes have a low repeatability of timing and wintering sites: Hoopoes leave the breeding grounds in a general direction, but due to changing environmental conditions between years in the Sahel, they return to the same region, but not necessarily to the exact same site. I suggest that after crossing the Sahara desert, Hoopoes settle in the first suitable place. What defines suitable is difficult to determine solely by using indirect measures such as satellite data and thus on-site studies will be needed to find out where exactly Hoopoes spend their winter, what they do and what they forage on.

To be at the right place at the right time, is very important. But the timing of a particular event is likely influenced by previous timing events. Birds are presumed to only be able to compensate by speeding up between events to some degree, which means that e.g. being late on one place, likely delays departure at the current stage and arrival at the next stage. Such dependencies have hardly been investigated to date. I therefore investigated the migration timing and potential for

compensation in Hoopoes. I could show that hardly any differences exist in timing between males and females, and indicate during which periods in the annual cycle birds could compensate for 'mistiming'. While the post-breeding and wintering period leave ample room for such compensation, it is hardly possible to compensate during autumn and spring migration and during the pre-breeding period. In parallel, variability in the timing of consecutive events decreased towards arrival in the breeding grounds. Furthermore, the timing of spring migration influenced reproductive success to some degree, since birds that started migration earlier and migrated faster, arrived earlier. In turn, birds that arrived earlier, started breeding earlier and had higher reproductive success. I conclude that the wintering period functions as a reset within the annual cycle, during which birds can "correct" previous 'mistiming', e.g. by speeding up moult. The moment of departure and a subsequent swift return to the breeding grounds increases the chances of reproductive success.

These last two chapters furthermore show that different selective pressures occur between autumn and spring migration, which thereby influence their respective repeatability. Autumn migration was much slower compared to spring migration and more depended on an individual's endogenous schedule, given the high repeatability in timing within an individual. To the contrary spring migration was hardly repeatable. I argue that the onset and duration of spring migration are much more under influence of differing environmental conditions between years, whereas birds aim to arrive at roughly the same date each year. But more research will be needed to establish how well Hoopoes (and other migrants) can cope with changing environmental conditions on their return migration to the breeding grounds.

Ultimately, we would like to understand how important migration is within the annual cycle and which consequences it has on fitness. Since timing events are linked and effects from one site could carry over to the next, we need to disentangle and quantify the relative effects of migration steps on breeding success. Therefore, we used a structural equation modelling approach and showed that the intrinsic quality of an individual is more important than migration, both in terms of timing and conditions encountered during winter. Combined with the chapter on timing, it shows that even though individual quality affects breeding success, the spring migration period may explain the variation in breeding success across individuals. The latter in turn is dependent on the timing of the whole migratory period as explained in the chapter on migration timing and compensation. For a successful progression of migration, an individual should be in good condition and be able to cope with adverse circumstances *en route* and in the wintering sites. Thus, individual quality and migratory progression seem to jointly orchestrate breeding success in Hoopoes.

In summary this thesis has contributed to the fast growing field of bird migration research by showing and quantifying how events throughout the annual cycle are linked. The low migratory connectivity in both Wrynecks and Hoopoes would make them less vulnerable for habitat changes, but the strong dependence of Wrynecks on extensive agricultural landscapes, might make them vulnerable. I could show that Hoopoes have a remarkable variety of migration patterns and these even change within an individual between years. This low repeatability was even found in first-time migrants, which suggests that Hoopoes could be described as opportunistic migrants. Choosing the right routes and wintering in the right places might enhance body condition, aid to proceed swiftly throughout the annual cycle and be most resilient to environmental stochasticity at all times and all places during the year and thus increase survival prospects. Especially the moment birds depart from winter, the condition they are in at that time and the conditions they experience on the way back to the breeding grounds may be crucial for the individual's survival and form a head start in the breeding grounds. Future research should thus aim at improving our understanding of the effect of the condition in which birds leave the wintering sites and how the condition changes during spring migration under influence of environmental stochasticity. Many questions still remain largely unresolved, especially for (near)passerines, including: what do wintering birds forage on, what determines the availability of these resources, is there competition for food that could constrain building up fat reserves before departure, what is the range in condition between individuals upon departure, where are stopovers being made on the return migration and how much time is spend stopping over, is it better to move fast and stop longer or move slower, but with shorter stops and how do e.g. influences by wind *en route* affect the route and time of arrival? Also more data is wanted on repeated tracks of the same individual to understand if and how experience could play a role in which routes to take and where to spend the non-breeding season.

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SUPPLEMENTARY MATERIAL

CHAPTER 2 – Appendix A: Description of the complete capture – recapture model with false occasions

General context

Capture-recapture models used to study the effect of an auxiliary marker, such as a second ring or neck band in birds, are usually multistate models with states reflecting the fact of wearing, or not, the auxiliary marker. of two probabilities, namely the loss of the secondary marker and survival and one step in detection, as described in the main text. In absence of recovery data, the following states can be used: “Alive with an auxiliary marker” (A+), “Alive without an auxiliary marker” (A-), “Dead” (D). The possible events recorded in the field are the following: a bird can be not detected (coded “0”), recaptured with the auxiliary marker (“1”) and recaptured without the auxiliary marker (“2”).

In the present study, we used geolocator as auxiliary marker. In order to retrieve the information stored on the geolocator in the course of a year, the goal is to recapture an individual and to remove the geolocator. The bird may or may not get then a new geolocator. Thus, the marker will not necessarily remain on an individual until it is dead. Therefore, the change of the individual’s state after first release will not only occur because of the loss of the device or the death of the individual, but also as a consequence of data retrieving. Thus, the state of an individual may be changed deterministically, which was handled in the data analyses by the addition of a dummy occasion (Fig. S1).

At the real occasion (hereafter *capture occasion*), a bird can either be captured or not, and if it is captured, its geolocator-state is assessed (G+, with or G-, without geolocator). Individuals that are captured can change its state due to removal and/or refitting of a geolocator. This deterministic change is modelled as the transition between the real and the false occasion. At the end of the false occasion (hereafter, *geolocator occasion*) the state of a captured bird changes from G+ or G- to S (equipped) or R (not equipped), Figure S2.

Individuals that are not captured are assigned to an unobservable state (Alive Elsewhere, AE), but we kept the signal of the geolocator status. Thus, an alive individual wearing a geolocator (G+) that was not captured during the breeding season was assigned to state AE+, similarly a G- individual becomes AE-.

To translate the fate diagram into matrices, we followed a two-step approach. First, we present the matrices used for each interval, either from capture to geolocator occasion or from

geolocator to capture occasion. Second, we pooled all the matrices together and provided the final matrices used for the present analysis.

Interval from capture to geolocator occasions.

For this interval the departing state of an individual was either: Alive with a geolocator (G+), Alive without a geolocator (G-) or Dead (D). The first step in the transition was to take into account whether the bird was detected or not, because geolocators could only be removed or put on captured birds. Thus, the capture matrix was:

$$\begin{array}{c} \\ G+ \\ G- \\ D \end{array} \begin{array}{c} \begin{array}{cccc} Capt & AE+ & AE- & D \end{array} \\ \begin{bmatrix} F & 1-F & 0 & 0 \\ F & 0 & 1-F & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{array},$$

with *F* the probability of the bird being captured. Because we knew which bird was captured in each year, we created 6 groups with 2 levels (captured / not captured), one for each year, to reflect this knowledge. As such we could fix the F parameter to 1 for individuals that were captured and to 0 otherwise.

Once we had distinguished between captured and non-captured individuals, we modelled the manipulation, as described in the following matrix:

$$\begin{array}{c} \\ Capt \\ AE+ \\ AE- \\ D \end{array} \begin{array}{c} \begin{array}{ccccc} S & R & AE+ & AE- & D \end{array} \\ \begin{bmatrix} \varepsilon & 1-\varepsilon & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \end{array},$$

with ε the proportion of captured birds which were equipped with a geolocator. This proportion is known for every year from field data, thus, we fixed ε to values 0.27, 0.41, 0.36, 0.38, 0.70 and 0.71 for year 2008, 2009, 2010, 2011, 2012 and 2013 respectively. Thus, at the end of the interval, the birds were released either in state S or R.

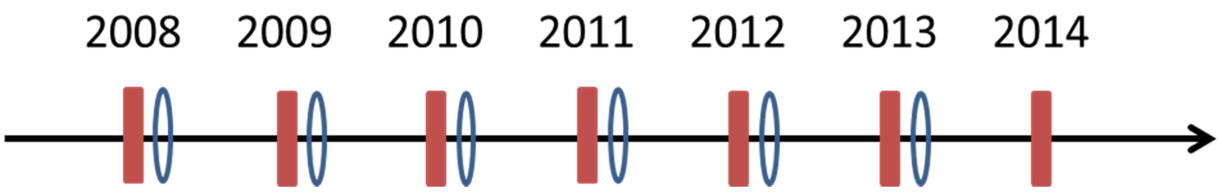

Figure S1: Sampling design in the dataset with both real and false occasions. Vertical bars and open circles represent real and false occasions, respectively.

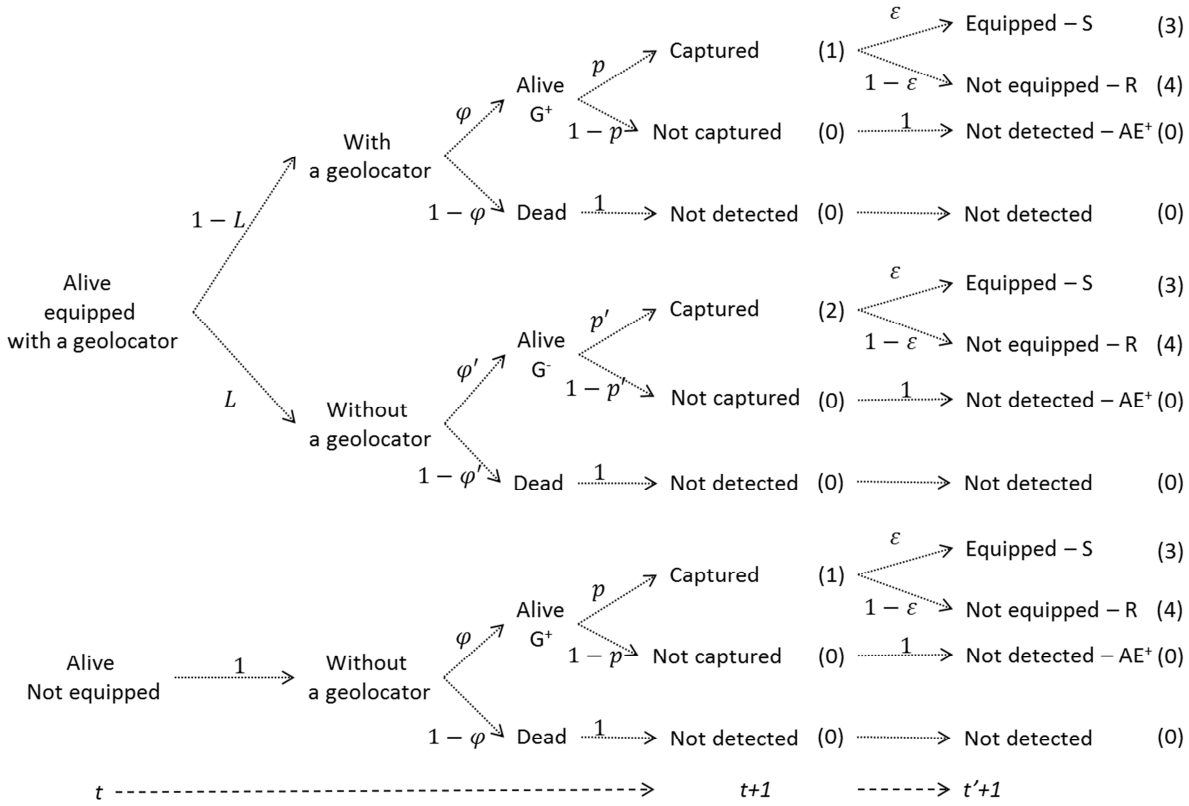

Figure S2: Fate diagram of a hoopoe marked with a metal band, and either equipped or not with a geolocator. *t*, *t+1* and *t'+1* correspond to the starting occasion, the subsequent real occasion and the subsequent dummy occasion, respectively. $\boldsymbol{L}$, φ, $\boldsymbol{p}$ represent the estimated loss, survival and detection probabilities, respectively. $\boldsymbol{\varepsilon}$ represents the proportion of birds that were equipped each year with a geolocator during the dummy occasion, which was fixed in the model. Numbers in brackets show the observed states at the real occasion (0,1,2) and the dummy occasion (0,3,4).

Concerning the detection part of the model, birds in states S and R were handled and as such their detection probability was 1, whereas it was 0 for the other states. Thereby, the detection matrix accounting for codes described at the fate diagram on the geolocator occasion was:

$$\begin{array}{c} \\ S \\ R \\ AE+ \\ AE- \\ D \end{array} \begin{array}{c} \begin{array}{ccc} 0 & 3 & 4 \end{array} \\ \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \end{bmatrix} \end{array}.$$

Interval from geolocator to capture occasions.

This interval represented the overwinter interval, thus the interval of principal interest. Individuals left the breeding ground in states S or R, or were outside the colony sites in states AE+ and AE-. The states at the end of this interval would be G+, G- and D. In the first step, we need to pool all individuals with (or without) geolocator together, thus a first matrix is:

$$\begin{array}{c} \\ S \\ R \\ AE+ \\ AE- \\ D \end{array} \begin{array}{c} \begin{array}{ccc} AG+ & AG- & D \end{array} \\ \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \end{array}.$$

Individuals wearing a geolocator or not were pooled under the state Alive with Geolocator (AG+) or Alive without Geolocator (AG-) respectively. The second step was to estimate the loss of the geolocator using the following matrix:

$$\begin{array}{c} \\ AG+ \\ AG- \\ D \end{array} \begin{array}{c} \begin{array}{ccc} G+ & G- & D \end{array} \\ \begin{bmatrix} 1-L & L & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \end{array},$$

with, *L* the probability that an individual will lose its geolocator.

Finally, the last step in the transition was the survival step:

$$\begin{array}{c} \\ G+ \\ G- \\ D \end{array} \begin{array}{c} \begin{array}{ccc} G+ & G- & D \end{array} \\ \begin{bmatrix} \varphi & 0 & 1-\varphi \\ 0 & \varphi' & 1-\varphi' \\ 0 & 0 & 1 \end{bmatrix} \end{array},$$

With φ and φ' the probabilities of survival for individuals with and without geolocator, respectively.

Regarding the detection probability, all individuals are assumed to be part of the same population, thus all individuals, conditionally they were alive, could be detected at the colony:

$$\begin{array}{c} \\ G+ \\ G- \\ D \end{array} \begin{array}{c} \begin{array}{ccc} 0 & 1 & 2 \end{array} \\ \begin{bmatrix} 1-p & p & 0 \\ 1-p' & 0 & p' \\ 1 & 0 & 0 \end{bmatrix} \end{array},$$

With p and p'the probabilities of recapture for individuals with and without geolocator, respectively.

General model and associated constrains

Now that we have our model for each kind of interval, we need to put them together to have our general model to estimate loss, survival and recapture probabilities while accounting for manipulating the states of the individuals.

For our general model, we thus dealt with the following states: “Alive with geolocator” (G+), “Alive without geolocator” (G-), “Alive and equipped” (S), “Alive but not equipped” (R), “Alive elsewhere with geolocator” (AE+), “Alive elsewhere without geolocator” (AE-) and “Dead” (D). The associated events were then: “not detected” (0), “captured with geolocator” (1), “captured without geolocator” (2), ”captured and equipped” (3) and “captured, not equipped” (4).

Regarding transitions, for the interval between capture and geolocators occasions, we had 2 steps (a capture and then a manipulation step) while for the interval between geolocator and the subsequent capture occasions, we had three (a population step, a loss step and finally, the survival step). For our general model, the idea was to pool together the capture and population matrices into an “availability” matrix, the manipulation and the loss matrices into a “geolocator” matrix, and finally, we had the survival matrix. Using a colour code we help the reader to keep track of the two parts of the pooled model.

a. The availability matrix

This matrix reflected the fact that all individuals in the population were available for detection or not, depending on the interval. Thus, the corresponding matrix is:

$$\begin{array}{c} \\ G+ \\ G- \\ S \\ R \\ AE+ \\ AE- \\ D \end{array}\begin{array}{c} \begin{array}{ccccccc} Capt & AE+ & AE- & AG+ & AG- & D \end{array} \\ \begin{bmatrix} F & 1-F & 0 & 0 & 0 \\ F & 0 & 1-F & & & \\ & & & 1 & 0 & \\ & & & 0 & 1 & \\ & 0 & & 1 & 0 & 0 \\ & & & 0 & 1 & \\ & 0 & & 0 & & 1 \end{bmatrix} \end{array}$$

The upper left corner of the matrix will be used for the interval from capture to geolocator occasions, while at the other intervals, the lower right part of the matrix will be used.

When used, the parameters in the upper left submatrix were fixed to 0 or 1 depending on whether a bird was captured or not. This information was kept using a group covariate for each year.

b. The geolocator matrix

This matrix was composed of a submatrix corresponding to the manipulation of the bird and by a submatrix to estimate loss probability:

$$\begin{array}{c} \\ Capt \\ AE+ \\ AE- \\ AG+ \\ AG- \\ D \end{array}\begin{array}{c} \begin{array}{ccccccc} S & R & AE+ & AE- & G+ & G- & D \end{array} \\ \begin{bmatrix} \varepsilon & 1-\varepsilon & 0 & 0 & & & \\ 0 & 0 & 1 & 0 & 0 & & 0 \\ 0 & 0 & 0 & 1 & & & \\ & & & & 1-L & L & \\ & 0 & & & 0 & 1 & 0 \\ & & & & & & \\ & 0 & & & 0 & & 1 \end{bmatrix} \end{array}$$

The proportion of birds equipped was fixed at each relevant interval (from capture to geolocator occasions, see above for used values) as the ratio of birds marked relative to the total number of birds captured. When the loss submatrix was not used (i.e. for the interval from capture to geolocator occasions), this parameter was fixed to 0.

c. The survival matrix

This survival step was only used for the interval from geolocator to capture occasion. Thus, we estimated survival only for states G+ and G-. For the other states, we simply used an identity submatrix to reflect that individuals can change states during this step:

$$\begin{array}{c} \\ S \\ R \\ AE+ \\ AE- \\ G+ \\ G- \\ D \end{array} \begin{array}{c} \begin{array}{cccccccc} G+ & G- & S & R & AE+ & AE- & D \end{array} \\ \begin{bmatrix} & & 1 & 0 & 0 & 0 & \\ & & 0 & 1 & 0 & 0 & \\ & 0 & 0 & 0 & 1 & 0 & 0 \\ & & 0 & 0 & 0 & 1 & \\ \varphi & 0 & & & & & 1-\varphi \\ 0 & \varphi' & & 0 & & & 1-\varphi' \\ 0 & & & 0 & & & 1 \end{bmatrix} \end{array}$$

For intervals were the survival submatrix was not used, the survival parameters were fixed to 1.

d. The detection matrix

The detection matrix was simpler to build: we just had to add the two matrices for each kind of interval:

$$\begin{array}{c} \\ G+ \\ G- \\ S \\ R \\ AE+ \\ AE- \\ D \end{array} \begin{array}{c} \begin{array}{ccccc} 0 & 1 & 2 & 3 & 4 \end{array} \\ \begin{bmatrix} 1-p & p & 0 & 0 & 0 \\ 1-p' & 0 & p' & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 \end{bmatrix} \end{array}$$

Due to the fact that manipulated birds were only captured birds, their detection is fixed to 1 for the geolocation occasion and to 0 otherwise. During the real capture occasion, the detection probabilities p and p' were estimated, but fixed to 0 for the other occasions.

Using these 3 steps-transition matrices and the detection matrix, we were able to estimate the loss and survival probabilities for hoopoes marked from 2008 to 2013 and recaptured from 2009 to 2014, while accounting for imperfect detection and manipulation of the states of individuals.

CHAPTER 2 – Appendix B: Model effect sizes for body condition, physiological state and reproductive performance

Table S1. Effect sizes and standard error (brackets) of all explanatory variables included in the final model on body condition upon arrival. Shown are resulting models for all years combined (2009-2014) and for each year separately. The intercept corresponds to females without a geolocator. For a description of the explanatory variables see Table 2.

Period		**Explanatory variables**				
	intercept	geolocator	sex	occupancy	breeding phase	onset breeding
2009-2014	0.470 (0.008)				0.0005 (0.0003)	
2009	0.577 (0.034)					-0.001 (0.0003)
2010	0.351 (0.052)				0.001 (0.0005)	0.01 (0.0004)
2011	0.410 (0.049)		-0.028 (0.013)			0.0009 (0.0004)
2012	0.537 (0.044)	0.033 (0.022)		-0.0005 (0.0004)	-0.002 (0.0011)	0.001 (0.0006)
2013	0.468 (0.008)					
2014	0.481 (0.006)					

Table S2. Effect sizes and standard error (brackets) of all explanatory variables included in the final model on A) baseline corticosterone and B) stress response. The intercept corresponds to 2nd year males without a geolocator. For a description of the variables used, see Table 2.

A: baseline corticosterone

Period		**Explanatory variables**							
	intercept	geolocator	age	body condition	onset breeding	occupancy	breeding phase	delta 1	capture time
2010-2013	16.29 (4.23)			-13.54 (6.75)	-0.049 (0.019)			1.97 (0.41)	-4.51 (2.05)
2010	-4.39 (1.93)			8.05 (3.89)				0.92 (0.31)	
2011	5.30 (1.67)		-0.261 (0.184)	-4.70 (2.49)			-0.035 (0.022)	0.36 (0.15)	-1.70 (0.78)
2012	4.14 (1.02)	0.35 (0.24)	-0.286 (0.188)		-0.029 (0.009)			0.32 (0.14)	
2013	2.64 (1.16)						-0.078 (0.053)	0.38 (0.15)	

B: stress response

Period		**Explanatory variables**							
	intercept	geolocator	age	body condition	onset breeding	occupancy	breeding phase	delta 2	capture time
2010-2013	46.65 (8.36)						-0.48 (0.32)		
2010	53.83 (12.38)								-46.63 (23.94)
2011	28.54 (34.45)		7.17 (4.04)	-87.84 (54.95)		-0.34 (0.09)		3.05 (1.43)	
2012	101.15 (34.21)	10.87 (7.86)	-6.73 (6.14)		-0.70 (0.27)				24.36 (21.54)
2013	57.52 (62.62)						-0.09 (0.55)		

Table S3. Effect sizes and standard error (brackets) of all explanatory variables included in the final model on A – territory occupancy, B – onset of breeding, C – brood success, D – number of fledglings in successful first broods and E – average weight of fledglings from successful first broods. Shown are outcomes resulting models for all years combined (2009-2014) and for each year separately. The intercept corresponds to females without a geolocator. For a description of the variables used, see Table 2.

A: territory occupancy

Period		**Explanatory variables**			
	intercept	geolocator	sex	body condition	onset breeding
2009-2014	98.75 (14.73)				-0.28 (0.13)
2009	120.74 (25.72)	11.21 (6.97)	11.91 (6.30)		-0.52 (0.22)
2010	114.08 (29.98)				-0.39 (0.26)
2011	68.57 (4.27)				
2012	203.66 (80.26)				-1.13 (0.67)
2013	56.50 (6.34)				
2014	60.38 (3.63)				

B: onset of breeding

Period		**Explanatory variables**			
	intercept	geolocator	sex	body condition	occupancy
2009-2014	122.10 (2.77)				-0.088 (0.039)
2009	209.53 (28.10)			-171.99 (57.89)	
2010	66.99 (30.17)			99.87 (61.67)	
2011	67.49 (34.07)	-17.20 (5.23)	8.40 (4.99)	102.07 (66.11)	
2012	135.40 (7.83	-5.92 (5.25)			-0.164 (0.085)
2013	125.7 (4.20)		-9.70 (6.30)		
2014	113.20 (1.87)				

C: brood success

Period		Explanatory variables				
	intercept	geolocator	sex	body condition	occupancy	onset breeding
2009-2014	0.59 (0.06)		0.096 (0.041)		0.004 (0.0008)	
2009	-0.03 (1.41)				0.048 (0.0273)	
2010	1.85 (0.62)				18.72 (3964.63)	
2011	2.23 (0.61)					
2012	61.07 (38.28)		-7.46 (5.89)	-107.69 (67.37)		
2013	-1.83 (1.62)		1.89 (1.39)		0.041 (0.0275)	
2014	2.22 (0.53)					

D: number of fledglings in successful first broods

Period		Explanatory variables				
	intercept	geolocator	sex	body condition	occupancy	onset breeding
2009-2014	7.66 (1.36)					-0.027 (0.011)
2009	-1.39 (3.83)		0.76 (0.49)	12.83 (7.97)		
2010	8.74 (2.15)					-0.033 (0.018)
2011	4.79 (0.29)	0.99 (0.52)				
2012	15.77 (6.87)	1.37 (0.86)	0.99 (0.76)	-25.80 (14.61)		
2013	4.54 (0.40)					
2014	4.50 (0.38)	0.88 (0.58)				

E: average weight of fledglings from successful first broods

Period		**Explanatory variables**				
	intercept	geolocator	sex	body condition	occupancy	onset breeding
2009-2014	80.46 (14.25)					-0.14 (0.12)
2009	35.22 (14.94)			74.43 (31.27)		
2010	74.21 (0.72)					
2011	87.86 (7.99)					-0.153 (0.067)
2012	75.43 (4.34)		8.96 (2.68)		-0.111 (0.052)	
2013	64.73 (4.30)				0.130 (0.065)	
2014	32.33 (22.46)			75.44 (46.53)		

Table S4. Estimated effects sizes of geolocator effects on various traits estimated with the models as shown in Tables S1, S2 and S3, which in addition included a geolocator effect. The complete data sets are analysed.

Trait	Effect	SE
Body condition upon arrival	-0.004	0.005
Baseline corticosterone	0.60	0.59
Stress response	3.54	3.66
Territory occupancy	-0.79	3.55
Onset of breeding	-0.74	1.97
Brood success	-0.06	0.04
Number of fledglings of fisrt brood	-0.27	0.32
Weight of nestlings	-4.22	3.33

CHAPTER 3 – Appendix

Table A. Timing of migration of adult Wrynecks from a Swiss (CH) and a German breeding population (DE). Indicated with a question mark in the arrival at breeding ground are birds of which the geolocator stopped working before returning back into the breeding grounds (data end states the last day of recording data). Differences between the median dates of the Swiss population against the bird from Germany were tested by one-sample signed rank tests (a) and one-sample t-tests (b) with DE-1 hypothesised as the population average (set to zero).

ID	Breeding ground	Non-breeding ground		Breeding ground
	Departure 2011	Arrival 2011	Departure 2012	Arrival 2012
CH-1	30 Aug	16 Oct	04 Mar	? data end 25 Mar
CH-2	30 Aug	10 Oct	02 Mar	06 Apr
CH-3	20 Aug	08 Oct	08 Mar	? data end 27 Mar
CH-4	20 Aug	02 Oct	06 Mar	? data end 01 Apr
CH-5	31 Aug	04 Oct	08 Mar	? data end 31 Mar
CH-6	19 Aug	06 Sept	08 Mar	? data end 03 Apr
CH-median	25 Aug	07 Oct	07 Mar	-
DE-1	14 Aug	02 Oct	15 Mar	08 Apr
Difference	Z = 2.21, P = 0.08 a	t = 0.014, P = 0.89 b	t = -7.38 P = 0.001 b	*NA*

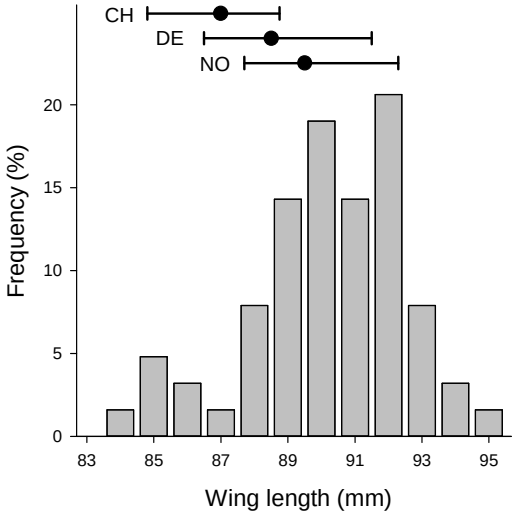

Figure A. Frequency distribution (in percentage) of wing lengths (mm) of wrynecks caught on passage in Col de Bretolet (Switzerland) and the wing lengths (median with 10% and 90% percentile) of two potential short-distance migrant populations (Switzerland, 'CH', and Germany, 'DE') and one potential long distance migrant population (Norway, 'NO').

CHAPTER 5 – Appendix 1: Overview of tested models on timing

Table S1. Overview of the explanatory variables used in each of the models; each model was run with and without year as fixed effect.

Timing of	Tested explanatory variables				
Departure from breeding grounds	Fledging date	#Broods	Brood Success	#Fledglings	Sex
Arrival in wintering grounds	Departure breeding	Direction autumn migration	Post-fledging period	Distance to breeding grounds	Sex
Departure from wintering grounds	Arrival wintering	Duration wintering			Sex
Arrival in breeding grounds	Departure wintering	Duration spring migration	Territory quality		Sex
Onset of breeding	Arrival breeding	Duration spring migration	Territory quality	Pre-laying period	Sex
#Fledglings first brood	Onset breeding	Duration spring migration	Territory quality	Arrival breeding	Sex
#Fledglings all broods	Onset breeding	Duration spring migration	Territory quality	Arrival breeding	Sex

Table S2. Tested models for the departure from the breeding grounds with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model dep13), model deviation (Dev) and the number of estimated parameters.

model	description	AIC	ΔAIC	dev	parameters
dep13	Fledging Date	436.08	0.00	7039	2
dep12	Number of Broods + Fledging Date	436.28	0.19	6777	3
dep15	Number of Fledglings + Fledging Date	436.49	0.40	6802	3
dep17	Brood Success + Fledging Date	437.73	1.65	6955	3
dep11	Number of Broods + Brood Success + Fledging Date	438.09	2.01	6705	4
dep4	Sex + Fledging Date	438.32	2.24	7029	3
dep14	Number of Broods + Number of Fledglings + Fledging Date	438.43	2.35	6745	4
dep3	Sex + Number of Broods + Fledging Date	438.67	2.58	6774	4
dep16	Brood Success + Number of Fledglings + Fledging Date	438.84	2.76	6795	4
dep6	Sex + Number of Fledglings + Fledging Date	438.89	2.80	6800	4
dep8	Sex + Brood Success + Fledging Date	440.08	3.99	6946	4
dep2	Sex + Number of Broods + Brood Success + Fledging Date	440.59	4.51	6703	5
dep10	Number of Broods + Brood Success + Number of Fledglings + Fledging Date	440.60	4.52	6704	5

dep5	Sex + Number of Broods + Number of Fledglings + Fledging Date	440.93	4.85	6743	5
dep21	Sex * Number of Broods + Fledging Date	441.05	4.97	6758	5
dep25	Sex * Number of Fledglings + Fledging Date	441.12	5.04	6767	5
dep7	Sex + Brood Success + Number of Fledglings + Fledging Date	441.34	5.26	6793	5
dep54	Fledging Date + Year	441.57	5.49	6509	6
dep20	Sex * Number of Broods + Brood Success + Fledging Date	443.11	7.03	6691	6
dep1	Sex + Number of Broods + Brood Success + Number of Fledglings + Fledging Date	443.20	7.12	6702	6
dep58	Brood Success + Fledging Date + Year	443.32	7.24	6397	7
dep24	Sex * Number of Fledglings + Number of Broods + Fledging Date	443.38	7.30	6723	6
dep22	Sex * Number of Broods + Number of Fledglings + Fledging Date	443.39	7.31	6724	6
dep26	Sex * Number of Fledglings + Brood Success + Fledging Date	443.70	7.62	6761	6
dep53	Number of Broods + Fledging Date + Year	443.81	7.73	6452	7
dep56	Number of Fledglings + Fledging Date + Year	444.05	7.97	6480	7
dep82	Sex + Fledging Date + Year	444.26	8.18	6505	7
dep52	Number of Broods + Brood Success + Fledging Date + Year	445.77	9.68	6351	8
dep19	Sex * Number of Broods + Brood Success + Number of Fledglings + Fledging Date	445.82	9.74	6689	7
dep23	Sex * Number of Fledglings + Number of Broods + Brood Success + Fledging Date	445.83	9.75	6690	7
dep96	Sex + Brood Success + Fledging Date + Year	446.17	10.09	6396	8
dep57	Brood Success + Number of Fledglings + Fledging Date + Year	446.17	10.09	6397	8
dep71	Sex + Number of Broods + Fledging Date + Year	446.63	10.55	6450	8
dep55	Number of Broods + Number of Fledglings + Fledging Date + Year	446.65	10.57	6452	8
dep94	Sex + Number of Fledglings + Fledging Date + Year	446.88	10.80	6478	8
dep51	Number of Broods + Brood Success + Number of Fledglings + Fledging Date + Year	448.27	12.19	6298	9
dep79	Number of Broods + Year	448.72	12.64	7396	6
dep60	Sex + Number of Broods + Brood Success + Fledging Date + Year	448.74	12.66	6350	9
dep95	Sex + Brood Success + Number of Fledglings + Fledging Date + Year	449.14	13.06	6396	9
dep66	Sex * Number of Fledglings + Fledging Date + Year	449.20	13.11	6402	9
dep62	Sex * Number of Broods + Fledging Date + Year	449.35	13.27	6420	9
dep93	Sex + Number of Broods + Number of Fledglings + Fledging Date + Year	449.61	13.52	6449	9
dep81	Number of Fledglings + Year	449.61	13.53	7515	6
dep84	Brood Success + Year	450.06	13.98	7575	6
dep72	Sex + Year	450.13	14.05	7585	6
dep37	Number of Broods	450.45	14.37	9098	2
dep78	Number of Broods + Brood Success + Year	451.19	15.11	7362	7
dep38	Number of Broods + Number of Fledglings	451.26	15.18	8856	3
dep50	Sex + Number of Broods + Brood Success + Number of Fledglings + Fledging Date + Year	451.38	15.30	6297	10

dep70	Sex + Number of Broods + Year	451.42	15.34	7392	7
dep80	Number of Broods + Number of Fledglings + Year	451.43	15.34	7393	7
dep41	Brood Success	451.45	15.37	9262	2
dep30	Sex	451.47	15.39	9266	2
dep39	Number of Fledglings	451.50	15.41	9270	2
dep67	Sex * Number of Fledglings + Brood Success + Fledging Date + Year	451.55	15.47	6316	10
dep61	Sex * Number of Broods + Brood Success + Fledging Date + Year	451.61	15.53	6323	10
dep83	Brood Success + Number of Fledglings + Year	451.64	15.56	7421	7
dep63	Sex * Number of Broods + Number of Fledglings + Fledging Date + Year	452.15	16.07	6419	10
dep65	Sex * Number of Fledglings + Number of Broods + Fledging Date + Year	452.19	16.11	6389	10
dep74	Sex + Number of Fledglings + Year	452.32	16.24	7512	7
dep29	Sex + Number of Broods	452.70	16.61	9086	3
dep36	Number of Broods + Brood Success	452.77	16.69	9098	3
dep76	Sex + Brood Success + Year	452.79	16.71	7575	7
dep35	Number of Broods + Brood Success + Number of Fledglings	453.01	16.93	8752	4
dep87	Sex * Number of Broods + Year	453.35	17.26	7271	8
dep31	Sex + Number of Broods + Number of Fledglings	453.65	17.56	8851	4
dep40	Brood Success + Number of Fledglings	453.71	17.63	9251	3
dep34	Sex + Brood Success	453.74	17.65	9256	3
dep32	Sex + Number of Fledglings	453.79	17.71	9265	3
dep77	Number of Broods + Brood Success + Number of Fledglings + Year	454.00	17.91	7356	8
dep69	Sex + Number of Broods + Brood Success + Year	454.03	17.95	7360	8
dep44	Sex * Number of Broods	454.18	18.10	8936	4
dep64	Sex * Number of Fledglings + Number of Broods + Brood Success + Fledging Date + Year	454.21	18.13	6250	11
dep73	Sex + Number of Broods + Number of Fledglings + Year	454.25	18.17	7390	8
dep59	Sex * Number of Broods + Brood Success + Number of Fledglings + Fledging Date + Year	454.46	18.38	6277	11
dep75	Sex + Brood Success + Number of Fledglings + Year	454.48	18.40	7420	8
dep91	Sex * Number of Fledglings + Year	454.79	18.71	7461	8
dep28	Sex + Number of Broods + Brood Success	455.11	19.03	9085	4
dep45	Sex * Number of Broods + Number of Fledglings	455.11	19.03	8687	5
dep27	Sex + Number of Broods + Brood Success + Number of Fledglings	455.50	19.42	8748	5
dep47	Sex * Number of Fledglings + Number of Broods	455.98	19.90	8823	5
dep86	Sex * Number of Broods + Brood Success + Year	456.07	19.99	7239	9
dep33	Sex + Brood Success + Number of Fledglings	456.10	20.01	9247	4
dep48	Sex * Number of Fledglings	456.20	20.12	9264	4
dep88	Sex * Number of Broods + Number of Fledglings + Year	456.28	20.20	7266	9

dep90	Sex * Number of Fledglings + Number of Broods + Year	456.52	20.44	7297	9
dep43	Sex * Number of Broods + Brood Success	456.69	20.61	8935	5
dep68	Sex + Number of Broods + Brood Success + Number of Fledglings + Year	456.96	20.88	7354	9
dep42	Sex * Number of Broods + Brood Success + Number of Fledglings	456.98	20.90	8571	6
dep92	Sex * Number of Fledglings + Brood Success + Year	457.05	20.97	7366	9
dep46	Sex * Number of Fledglings + Number of Broods + Brood Success	457.82	21.73	8700	6
dep49	Sex * Number of Fledglings + Brood Success	458.60	22.52	9245	5
dep85	Sex * Number of Broods + Brood Success + Number of Fledglings + Year	459.16	23.08	7236	10
dep89	Sex * Number of Fledglings + Number of Broods + Brood Success + Year	459.41	23.32	7267	10

Table S3. Tested models for the arrival in the wintering grounds with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model arr56), model deviation (Dev) and the number of estimated parameters.

model	**description**	**AICc**	**ΔAICc**	**dev**	**parameters**
arr56	Departure from Breeding Grounds + Post-fledging Period	442.27	0.00	9683	3
arr1	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Year	442.72	0.45	8193	10
arr50	Departure from Breeding Grounds	443.06	0.78	10259	2
arr71	Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period	443.59	1.31	9484	4
arr66	Distance to Breeding Grounds + Departure from Breeding Grounds	443.82	1.54	9963	3
arr53	Sex + Departure from Breeding Grounds + Post-fledging Period	444.44	2.17	9635	4
arr41	Direction Autumn Migration + Departure from Breeding Grounds	444.58	2.30	9660	4
arr47	Sex + Departure from Breeding Grounds	445.11	2.83	10204	3
arr44	Direction Autumn Migration + Departure from Breeding Grounds + Post-fledging Period	445.19	2.92	9321	5
arr7	Departure from Breeding Grounds + Year	445.22	2.95	8881	6
arr55	Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds	445.32	3.04	9343	5
arr67	Sex + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period	445.94	3.66	9451	5
arr63	Sex + Distance to Breeding Grounds + Departure from Breeding Grounds	446.06	3.79	9929	4
arr60	Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period	446.39	4.12	9075	6
arr40	Sex + Direction Autumn Migration + Departure from Breeding Grounds	446.70	4.42	9585	5
arr6	Direction Autumn Migration + Departure from Breeding Grounds + Year	446.89	4.61	8248	8
arr15	Departure from Breeding Grounds + Post-fledging Period + Year	446.94	4.66	8710	7
arr43	Sex + Direction Autumn Migration + Departure from Breeding Grounds + Post-fledging Period	447.48	5.20	9259	6
arr57	Post-fledging Period	447.64	5.37	11168	2

arr3	Sex + Departure from Breeding Grounds + Year	447.65	5.38	8825	7
arr51	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds	447.68	5.41	9295	6
arr8	Distance to Breeding Grounds + Departure from Breeding Grounds + Year	447.98	5.71	8880	7
arr31	Post-fledging Period + Year	448.26	5.99	9395	6
arr45	Direction Autumn Migration + Post-fledging Period	448.88	6.60	10460	4
arr58	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period	448.91	6.64	9034	7
arr73	Distance to Breeding Grounds + Post-fledging Period	449.45	7.18	11059	3
arr11	Sex + Departure from Breeding Grounds + Post-fledging Period + Year	449.53	7.25	8661	8
arr2	Sex + Direction Autumn Migration + Departure from Breeding Grounds + Year	449.61	7.34	8202	9
arr14	Direction Autumn Migration + Departure from Breeding Grounds + Post-fledging Period + Year	449.62	7.35	8204	9
arr54	Sex + Post-fledging Period	449.80	7.52	11130	3
arr16	Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period + Year	449.81	7.54	8707	8
arr5	Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Year	449.85	7.58	8238	9
arr30	Direction Autumn Migration + Post-fledging Period + Year	450.21	7.93	8771	8
arr61	Direction Autumn Migration + Distance to Breeding Grounds + Post-fledging Period	450.38	8.10	10261	5
arr4	Sex + Distance to Breeding Grounds + Departure from Breeding Grounds + Year	450.53	8.26	8824	8
arr27	Sex + Post-fledging Period + Year	450.75	8.48	9347	7
arr32	Distance to Breeding Grounds + Post-fledging Period + Year	450.99	8.72	9389	7
arr42	Sex + Direction Autumn Migration + Post-fledging Period	451.17	8.89	10412	5
arr52	Direction Autumn Migration + Fledging Date	451.58	9.31	9662	4
arr70	Sex + Distance to Breeding Grounds + Post-fledging Period	451.75	9.48	11032	4
arr10	Sex + Direction Autumn Migration + Departure from Breeding Grounds + Post-fledging Period + Year	452.52	10.24	8162	10
arr12	Sex + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period + Year	452.53	10.26	8658	9
arr13	Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period + Year	452.76	10.49	8199	10
arr59	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Post-fledging Period	452.86	10.59	10230	6
arr26	Sex + Direction Autumn Migration + Post-fledging Period + Year	452.99	10.72	8732	9
arr68	Direction Autumn Migration + Distance to Breeding Grounds + Fledging Date	453.03	10.75	9474	5
arr29	Direction Autumn Migration + Distance to Breeding Grounds + Post-fledging Period + Year	453.08	10.81	8747	9
arr28	Sex + Distance to Breeding Grounds + Post-fledging Period + Year	453.61	11.34	9342	8
arr49	Sex + Direction Autumn Migration + Fledging Date	453.81	11.54	9610	5
arr38	Direction Autumn Migration + Year	454.20	11.92	8776	7
arr48	Direction Autumn Migration	454.92	12.64	10729	3
arr65	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Fledging Date	455.48	13.21	9444	6
arr22	Direction Autumn Migration + Fledging Date + Year	455.48	13.21	8527	8
arr9	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Departure from Breeding Grounds + Post-fledging Period + Year	455.81	13.53	8157	11

arr25	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Post-fledging Period + Year	456.01	13.74	8708	10
arr64	Direction Autumn Migration + Distance to Breeding Grounds	456.14	13.87	10498	4
arr34	Sex + Direction Autumn Migration + Year	456.81	14.54	8736	8
arr37	Direction Autumn Migration + Distance to Breeding Grounds + Year	456.91	14.63	8751	8
arr46	Sex + Direction Autumn Migration	457.08	14.81	10678	4
arr74	Fledging Date	457.31	15.03	10283	2
arr18	Sex + Direction Autumn Migration + Fledging Date + Year	458.23	15.96	8488	9
arr21	Direction Autumn Migration + Distance to Breeding Grounds + Fledging Date + Year	458.45	16.18	8522	9
arr62	Sex + Direction Autumn Migration + Distance to Breeding Grounds	458.52	16.25	10470	5
arr78	Distance to Breeding Grounds + Fledging Date	458.71	16.43	10115	3
arr72	Sex + Fledging Date	459.22	16.94	10208	3
arr33	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Year	459.65	17.38	8710	9
arr76	Sex + Distance to Breeding Grounds + Fledging Date	460.85	18.57	10065	4
arr23	Fledging Date + Year	461.18	18.91	9239	6
arr17	Sex + Direction Autumn Migration + Distance to Breeding Grounds + Fledging Date + Year	461.33	19.06	8482	10
arr35	Sex + Year	462.49	20.22	9534	6
arr19	Sex + Fledging Date + Year	463.32	21.04	9141	7
arr39	Distance to Breeding Grounds + Year	463.50	21.23	9630	6
arr24	Distance to Breeding Grounds + Fledging Date + Year	463.85	21.57	9229	7
arr77	Distance to Breeding Grounds	464.16	21.88	11622	2
arr69	Sex	464.82	22.55	11761	2
arr36	Sex + Distance to Breeding Grounds + Year	465.67	23.40	9534	7
arr20	Sex + Distance to Breeding Grounds + Fledging Date + Year	466.12	23.84	9134	8
arr75	Sex + Distance to Breeding Grounds	466.28	24.01	11581	3

Table S4. Tested models for the departure from the wintering grounds with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model dep5), model deviation (Dev) and number of estimated parameters. All models were also tested including year as fixed effect.

model	**description**	**AICc**	**ΔAICc**	**dev**	**parameters**
dep5	Wintering Duration	363.3768	0	4173.3	2
dep2	Sex + Wintering Duration	365.6101	2.2333	4161.2	3
dep6	Wintering Duration + Year	368.6439	5.2671	3774	6
dep4	Arrival in Wintering Grounds	369.0456	5.6688	4685.1	2

dep7	Sex + Wintering Duration + Year	371.1696	7.7928	3748	7
dep1	Sex + Arrival in Wintering Grounds	371.2506	7.8738	4668.9	3
dep8	Arrival in Wintering Grounds + Year	376.0753	12.6985	4392	6
dep3	Sex	378.4983	15.1215	4982.4	2
dep9	Sex + Arrival in Wintering Grounds + Year	378.6638	15.287	4367	7
dep10	Sex + Year	386.6031	23.2263	4783	6

Table S5. Tested models for the arrival in the breeding grounds with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model arr1), model deviation (Dev) and number of estimated parameters. All models were also tested including year as fixed effect.

model	**description**	**AICc**	**ΔAICc**	**dev**	**parameters**
arr1	Duration Spring Migration	318.1098	0	2353	2
arr2	Duration Spring Migration + Occupancy	320.2349	2.1251	2339	3
arr20	Duration Spring Migration + Sex	320.384	2.2742	2346	3
arr19	Duration Spring Migration + Sex + Occupancy	322.6753	4.5655	2334	4
arr6	Duration Spring Migration + Year	325.4722	7.3624	2204	6
arr16	Departure from Wintering	326.4097	8.2999	2818	2
arr8	Duration Spring Migration + Sex + Year	328.3989	10.2891	2203	7
arr7	Duration Spring Migration + Occupancy + Year	328.4093	10.2995	2203	7
arr18	Departure from Wintering + Occupancy	328.6269	10.5171	2807	3
arr17	Departure from Wintering + Sex + Occupancy	331.0775	12.9677	2802	4
arr9	Duration Spring Migration + Sex + Occupancy + Year	331.4949	13.3851	2202	8
arr5	Occupancy	332.7228	14.613	3233	2
arr4	Sex	332.8536	14.7438	3242	2
arr11	Departure from Wintering + Year	333.3879	15.2781	2617	6
arr3	Sex + Occupancy	335.0306	16.9208	3226	3
arr13	Departure from Wintering + Occupancy + Year	336.2008	18.091	2610	7
arr15	Departure from Wintering + Sex + Occupancy + Year	339.2524	21.1426	2607	8
arr10	Occupancy + Year	339.7812	21.6714	3008	6
arr12	Sex + Year	339.827	21.7172	3011	6
arr14	Sex + Occupancy + Year	342.6756	24.5658	3004	7

Table S6. Tested models for the onset of breeding with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model strt5), model deviation (Dev) and the number of estimated parameters.

model	description	AICc	ΔAICc	dev	parameters
strt5	Duration Spring Migration + Pre-laying Period + Occupancy	353.79	0.00	3427	4
strt28	Duration Spring Migration + Sex + Pre-laying Period + Occupancy	355.60	1.82	3381	5
strt7	Duration Spring Migration + Pre-laying Period	356.93	3.14	3866	3
strt29	Duration Spring Migration + Sex + Pre-laying Period	358.74	4.96	3823	4
strt34	Duration Spring Migration + Pre-laying Period + Occupancy + Year	361.57	7.78	3174	8
strt21	Pre-laying Period + Occupancy	361.94	8.15	4217	3
strt57	Duration Spring Migration + Sex + Pre-laying Period + Occupancy + Year	362.66	8.87	3066	9
strt9	Sex + Pre-laying Period + Occupancy	363.85	10.06	4182	4
strt36	Duration Spring Migration + Pre-laying Period + Year	364.37	10.58	3584	7
strt58	Duration Spring Migration + Sex + Pre-laying Period + Year	365.28	11.50	3466	8
strt25	Pre-laying Period	366.70	12.92	4909	2
strt10	Sex + Pre-laying Period	368.61	14.83	4879	3
strt50	Pre-laying Period + Occupancy + Year	369.34	15.56	3973	7
strt38	Sex + Pre-laying Period + Occupancy + Year	369.95	16.16	3847	8
strt24	Arrival in Breeding Grounds + Occupancy	370.60	16.82	5130	3
strt54	Pre-laying Period + Year	371.97	18.19	4466	6
strt20	Arrival in Breeding Grounds + Duration Spring Migration + Occupancy	372.02	18.24	5029	4
strt39	Sex + Pre-laying Period + Year	372.39	18.61	4328	7
strt22	Arrival in Breeding Grounds + Sex + Occupancy	372.48	18.69	5080	4
strt16	Arrival in Breeding Grounds	373.84	20.05	5712	2
strt19	Arrival in Breeding Grounds + Duration Spring Migration + Sex + Occupancy	373.92	20.13	4969	5
strt15	Arrival in Breeding Grounds + Duration Spring Migration	375.01	21.23	5588	3
strt18	Arrival in Breeding Grounds + Sex	375.31	21.53	5629	3
strt14	Arrival in Breeding Grounds + Duration Spring Migration + Sex	376.47	22.69	5492	4
strt27	Occupancy	376.91	23.13	6306	2
strt53	Arrival in Breeding Grounds + Occupancy + Year	377.72	23.94	4781	7
strt8	Duration Spring Migration + Occupancy	378.64	24.86	6214	3
strt12	Sex + Occupancy	379.28	25.49	6303	3
strt51	Arrival in Breeding Grounds + Sex + Occupancy + Year	380.23	26.44	4755	8
strt49	Arrival in Breeding Grounds + Duration Spring Migration + Occupancy + Year	380.26	26.48	4724	8

strt45	Arrival in Breeding Grounds + Year	382.00	28.21	5507	6
strt48	Arrival in Breeding Grounds + Duration Spring Migration + Sex + Occupancy + Year	382.92	29.13	4694	9
strt44	Arrival in Breeding Grounds + Duration Spring Migration + Year	383.81	30.03	5379	7
strt56	Occupancy + Year	384.02	30.24	5901	6
strt47	Arrival in Breeding Grounds + Sex + Year	384.11	30.32	5458	7
strt2	Duration Spring Migration	384.18	30.40	7318	2
strt23	Sex	385.13	31.34	7483	2
strt37	Duration Spring Migration + Occupancy + Year	385.82	32.04	5772	7
strt43	Arrival in Breeding Grounds + Duration Spring Migration + Sex + Year	386.06	32.28	5324	8
strt3	Duration Spring Migration + Sex	386.46	32.68	7306	3
strt41	Sex + Occupancy + Year	386.83	33.05	5897	7
strt31	Duration Spring Migration + Year	391.84	38.06	6941	6
strt52	Sex + Year	392.54	38.76	7054	6
strt32	Duration Spring Migration + Sex + Year	394.73	40.95	6939	7

Table S7. Tested models for the number of fledglings in the first brood after arrival with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model succ30), model deviation (Dev) and number of estimated parameters. All models were also tested including year as fixed effect.

model	**description**	**AICc**	**ΔAICc**	**dev**	**parameters**
succ30	Occupancy+Arrival in Breeding Grounds	210.0633	0	180.87	3
succ48	Onset of Breeding+Occupancy+sex+Arrival in Breeding Grounds	210.3475	0.2842	167.4	5
succ10	Onset of Breeding+Occupancy+Arrival in Breeding Grounds	210.444	0.3807	180.8	4
succ56	Duration Spring Migration+Occupancy+sex	210.6267	0.5634	168.13	4
succ46	Duration Spring Migration+Occupancy+sex+Arrival in Breeding Grounds	211.8336	1.7703	166.85	5
succ26	Onset of Breeding+Arrival in Breeding Grounds	211.9239	1.8606	200.35	3
succ14	Duration Spring Migration+Occupancy	212.2022	2.1389	182.84	3
succ4	Duration Spring Migration+Occupancy+Arrival in Breeding Grounds	212.4401	2.3768	179.61	4
succ32	sex+Arrival in Breeding Grounds	212.7848	2.7215	185.26	3
succ24	Duration Spring Migration+Onset of Breeding+Occupancy+Arrival in Breeding Grounds	212.8115	2.7482	179.57	5
succ2	Duration Spring Migration+Onset of Breeding+Occupancy+sex	212.8985	2.8352	167.6	5
succ16	Duration Spring Migration+sex	213.0812	3.0179	184.83	3
succ52	Duration Spring Migration+Onset of Breeding+sex	213.6642	3.6009	184.08	4
succ44	Duration Spring Migration+Onset of Breeding+sex+Arrival in Breeding Grounds	214.1292	4.0659	183.79	5

succ54	Duration Spring Migration+Onset of Breeding+Arrival in Breeding Grounds	214.198	4.1347	199.28	4
succ42	Arrival in Breeding Grounds	214.2054	4.1421	201.9	2
succ50	Duration Spring Migration+Onset of Breeding+Occupancy	214.2454	4.1821	182.18	4
succ34	Duration Spring Migration	214.9077	4.8444	201.61	2
succ12	Duration Spring Migration+Onset of Breeding	215.1062	5.0429	200.84	3
succ6	Duration Spring Migration+sex+Arrival in Breeding Grounds	215.266	5.2027	184.81	4
succ28	Occupancy+sex	215.623	5.5597	182.8	3
succ18	Duration Spring Migration+Arrival in Breeding Grounds	216.5369	6.4736	200.95	3
succ29	year + Occupancy+Arrival in Breeding Grounds	217.8744	7.8111	164	7
succ40	sex	217.9095	7.8462	200.72	2
succ8	Onset of Breeding+Occupancy+sex	218.0967	8.0334	180.59	4
succ38	Occupancy	218.2652	8.2019	202.15	2
succ25	year + Onset of Breeding+Arrival in Breeding Grounds	219.1533	9.09	181	3
succ9	year + Onset of Breeding+Occupancy+Arrival in Breeding Grounds	219.2676	9.2043	167	4
succ22	Onset of Breeding+sex	219.6292	9.5659	200.68	3
succ41	year + Arrival in Breeding Grounds	220.59	10.5267	199	2
succ20	Onset of Breeding+Occupancy	220.6323	10.569	199.07	3
succ55	year + Duration Spring Migration+Occupancy+sex	220.6993	10.636	163	8
succ47	year + Onset of Breeding+Occupancy+sex+Arrival in Breeding Grounds	220.734	10.6707	158	5
succ3	year + Duration Spring Migration+Occupancy+Arrival in Breeding Grounds	220.7552	10.6919	174	4
succ13	year + Duration Spring Migration+Occupancy	220.7668	10.7035	174	7
succ31	year + sex+Arrival in Breeding Grounds	220.9743	10.911	184	3
succ15	year + Duration Spring Migration+sex	221.6802	11.6169	185	3
succ45	year + Duration Spring Migration+Occupancy+sex+Arrival in Breeding Grounds	221.9699	11.9066	163	5
succ33	year + Duration Spring Migration	222.0342	11.9709	202	2
succ53	year + Duration Spring Migration+Onset of Breeding+Arrival in Breeding Grounds	222.064	12.0007	180	4
succ23	year + Duration Spring Migration+Onset of Breeding+Occupancy+Arrival in Breeding Grounds	222.2357	12.1724	166	5
succ36	Onset of Breeding	222.3258	12.2625	222.48	2
succ51	year + Duration Spring Migration+Onset of Breeding+sex	223.1832	13.1199	178	4
succ11	year + Duration Spring Migration+Onset of Breeding	223.3981	13.3348	193	3
succ17	year + Duration Spring Migration+Arrival in Breeding Grounds	223.4458	13.3825	199	3
succ43	year + Duration Spring Migration+Onset of Breeding+sex+Arrival in Breeding Grounds	223.4803	13.417	170	5
succ49	year + Duration Spring Migration+Onset of Breeding+Occupancy	223.6343	13.571	180	4
succ1	year + Duration Spring Migration+Onset of Breeding+Occupancy+sex	223.7091	13.6458	166	5
succ5	year + Duration Spring Migration+sex+Arrival in Breeding Grounds	223.9896	13.9263	184	4

succ27	year + Occupancy+sex	225.827	15.7637	183	3
succ39	year + sex	227.5846	17.5213	201	2
succ37	year + Occupancy	227.6129	17.5496	202	2
succ7	year + Onset of Breeding+Occupancy+sex	228.788	18.7247	183	4
succ21	year + Onset of Breeding+sex	229.8852	19.8219	198	3
succ19	year + Onset of Breeding+Occupancy	230.3827	20.3194	202	3
succ35	year + Onset of Breeding	232.0676	22.0043	219	2

Table S8. Tested models for the total number of fledglings after arrival with the relative corrected Aikaike Information Criterion (AICc) distance to the best model (model succ7), model deviation (Dev) and the number of estimated parameters.

model	**description**	**AICc**	**ΔAICc**	**dev**	**parameters**
succ26	Onset of Breeding+Arrival in Breeding Grounds	241.4618	0	330	3
succ10	Onset of Breeding+Occupancy+Arrival in Breeding Grounds	242.8073	1.3455	323	4
succ54	Duration Spring Migration+Onset of Breeding+Arrival in Breeding Grounds	243.5439	2.0821	328	4
succ48	Onset of Breeding+Occupancy+sex+Arrival in Breeding Grounds	243.9306	2.4688	313	5
succ44	Duration Spring Migration+Onset of Breeding+sex+Arrival in Breeding Grounds	244.7064	3.2446	318	5
succ24	Duration Spring Migration+Onset of Breeding+Occupancy+Arrival in Breeding Grounds	244.9932	3.5314	320	5
succ52	Duration Spring Migration+Onset of Breeding+sex	245.5099	4.0481	341	4
succ12	Duration Spring Migration+Onset of Breeding	245.6588	4.197	360	3
succ50	Duration Spring Migration+Onset of Breeding+Occupancy	247.3024	5.8406	354	4
succ2	Duration Spring Migration+Onset of Breeding+Occupancy+sex	247.3275	5.8657	336	5
succ25	year + Onset of Breeding+Arrival in Breeding Grounds	249.8961	8.4343	315	3
succ9	year + Onset of Breeding+Occupancy+Arrival in Breeding Grounds	251.3385	9.8767	305	4
succ53	year + Duration Spring Migration+Onset of Breeding+Arrival in Breeding Grounds	251.8569	10.3951	309	4
succ22	Onset of Breeding+sex	252.6552	11.1934	384	3
succ47	year + Onset of Breeding+Occupancy+sex+Arrival in Breeding Grounds	252.9819	11.5201	296	5
succ23	year + Duration Spring Migration+Onset of Breeding+Occupancy+Arrival in Breeding Grounds	253.2282	11.7664	298	5
succ43	year + Duration Spring Migration+Onset of Breeding+sex+Arrival in Breeding Grounds	253.5784	12.1166	300	5

succ8	Onset of Breeding+Occupancy+sex	253.9144	12.4526	374	4
succ36	Onset of Breeding	253.955	12.4932	413	2
succ30	Occupancy+Arrival in Breeding Grounds	254.642	13.1802	432	3
succ51	year + Duration Spring Migration+Onset of Breeding+sex	254.6627	13.2009	327	4
succ56	Duration Spring Migration+Occupancy+sex	254.6734	13.2116	411	4
succ11	year + Duration Spring Migration+Onset of Breeding	254.7351	13.2733	348	3
succ14	Duration Spring Migration+Occupancy	254.8174	13.3556	434	3
succ20	Onset of Breeding+Occupancy	254.9799	13.5181	402	3
succ49	year + Duration Spring Migration+Onset of Breeding+Occupancy	256.1202	14.6584	337	4
succ1	year + Duration Spring Migration+Onset of Breeding+Occupancy+sex	256.3372	14.8754	317	5
succ32	sex+Arrival in Breeding Grounds	256.6012	15.1394	450	3
succ16	Duration Spring Migration+sex	256.729	15.2672	451	3
succ4	Duration Spring Migration+Occupancy+Arrival in Breeding Grounds	257.0865	15.6247	432	4
succ34	Duration Spring Migration	257.1655	15.7037	478	2
succ42	Arrival in Breeding Grounds	257.1735	15.7117	478	2
succ46	Duration Spring Migration+Occupancy+sex+Arrival in Breeding Grounds	257.25	15.7882	411	5
succ28	Occupancy+sex	258.1236	16.6618	428	3
succ38	Occupancy	259.0165	17.5547	457	2
succ6	Duration Spring Migration+sex+Arrival in Breeding Grounds	259.0871	17.6253	450	4
succ18	Duration Spring Migration+Arrival in Breeding Grounds	259.5377	18.0759	478	3
succ21	year + Onset of Breeding+sex	259.6079	18.1461	356	3
succ7	year + Onset of Breeding+Occupancy+sex	260.1839	18.7221	340	4
succ40	sex	260.3811	18.9193	469	2
succ35	year + Onset of Breeding	261.3263	19.8645	390	2
succ19	year + Onset of Breeding+Occupancy	261.3503	19.8885	369	3
succ29	year + Occupancy+Arrival in Breeding Grounds	261.461	19.9992	399	7
succ13	year + Duration Spring Migration+Occupancy	261.4644	20.0026	399	7
succ55	year + Duration Spring Migration+Occupancy+sex	262.0414	20.5796	380	8
succ3	year + Duration Spring Migration+Occupancy+Arrival in Breeding Grounds	263.8769	22.4151	395	4
succ27	year + Occupancy+sex	264.4346	22.9728	393	3

succ37	year + Occupancy	264.7003	23.2385	418	2
succ45	year + Duration Spring Migration+Occupancy+sex+Arrival in Breeding Grounds	265.0452	23.5834	379	5
succ33	year + Duration Spring Migration	265.3949	23.9331	459	2
succ41	year + Arrival in Breeding Grounds	265.5682	24.1064	460	2
succ15	year + Duration Spring Migration+sex	265.7088	24.247	436	3
succ31	year + sex+Arrival in Breeding Grounds	265.8016	24.3398	436	3
succ17	year + Duration Spring Migration+Arrival in Breeding Grounds	268.2276	26.7658	459	3
succ5	year + Duration Spring Migration+sex+Arrival in Breeding Grounds	268.6891	27.2273	435	4
succ39	year + sex	268.9058	27.444	454	2

CHAPTER 7 – Appendix A: Number of hoopoes marked and recaptured by sex and year

Table A1: Number of hoopoes marked from 2009 to 2013 that were recaptured one year later with data on the geolocator, divided by sex and year.

Marking year	Sex		
	Female	Male	*Total*
2009	10	4	*14*
2010	1	5	*6*
2011	3	5	*8*
2012	9	7	*16*
2013	4	6	*10*
Total	*27*	*27*	54

CHAPTER 7 – Appendix B: Complete R code for the structural equation model

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## Structural Equation Model to investigate carry-over effects in Hoopoes
##########################################################################
## set the working directory
setwd("D:/Dropbox/post-doc/hoopoe/Carry-over effect/analysis/5th run")

## import data
donnees <- read.table("GS_Carry-Over_Data_FINAL_RVW.csv",sep=";",header=T)

## removing non-useful data (geol, ring, yeart, year t+1, sex, unknown variables)
data1 <- donnees[,-c(1,2,3,4,5,28,29,30,31)]
# We then remove the unused variables (Pfledg,Pstrt,WiNDVI_cum,WiLoc,SpArr,Bsfledg).
data1 <- data1[,-c(3,4,11,14,16,22)]
# due to lots of variation among magnitude of data and
# because we were more interested in impact of change and relative effect,
# we decided to scale all variables. However, ordered categorized data can not be scale.
# Thus, we scaled continuous data only.
data2 <- data1[,-c(2,16)] # removing Pbrood and Bsbrood
data2 <- scale(data2,scale=T,center=T)
# Then we pooled all data back together
data3 <- cbind(data1[,c(2,16)],data2)
data.final <-
data3[,c("Pfledg1","FaDep","WiArr","WiNDVI_median","SpDep","Bsfledg1","Pbrood","Bsbrood","FaDur","WiD
ur","WiNDVI_delta","SpDur")]
data.sem <- as.matrix(data.final)

N <- dim(data.sem)[1] # number of individuals
V <- dim(data.sem)[2] # number of variables
L <- 6            # number of latent variables (exogenous + endogenous), also the number of fixed lambda
P <- 2            # number of ordered categorized variable
######################
### Model requirement

## create matrix with the value of estimated threshold for categorized variables Pbrood
# estimation of threshold following the method in Lee & Song 2012, Chap 5
# first and last threshold are set asymptoticly large
# other thresholf are the product of Normal distrib function and the cumulative frequency of category

table(data.sem[,7]) # give the number of occurence for each cat
table(data.sem[,8]) # give the number of occurence for each cat

# use the frequency to fill the corresponding row in the matrix
thd <- matrix(NA,nrow=V,ncol=5)
thd[7,] <- c(-200,qnorm(29/54),qnorm(52/54),100,200)        # freq of categ for Pbrood
thd[8,] <- c(-200,qnorm(23/54),qnorm(51/54),qnorm(53/54),200)  # freq of categ for Bsbrood
############################
### explanation of the Model
```

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# We want to evaluate direct and indirect effects of several steps of anual life cycle
# of a migrant bird species.
# The important step are thus the previous breeding season, fall and spring migration, and wintering.
# Wintering was divided into timing and condition of wintering. Condition of wintering were obtained
# by using freely available large-scale index (NDVI). For each individual, we sampled over the location
# of wintering from October to February to obtain a median value of NDVI over the 5 months and
# we computed a temporal variation index by substracting the median of October (arrival date) to the median
# of February (departure date).
# All other timing variable were obtained from an analysis of geolocator data from equipped and
# recaptured birds. Measures from breeding were obtained at the colony in Valais.
# To investigate the carry-over effect, we defined, for each step a latent variable:
# - xi[i,1] is the latent variable representing the previous breeding
#     and its indicators are:
#     Pfledg1 (number of fledglings of the 1st brood)
#     Pbrood  (number of broods)
# - xi[i,2] is the Fall Migration latent variable
#     FaDep (date of departure)
#     FaDur (duration of migration)
# - xi[i,3] is the winter Schedule latent variable
#     WiArr (date of arrival on wintering ground)
#     WiDur (duration)
# - xi[i,4] is the Winter Condition latent variable
#     WiNDVI_median
#     WiNDVI_delta
# - xi[i,5] is the Spring migration latent variable
#     SpDep (date of departure)
#     SpDur (duration)
#
# All of these 6 latent variables are assumed to have effect on the Breeding success
# - eta[i,1] is the Breeding Success depedent latent variable
#     Bsfledg1 (number of fledglings of the 1st brood)
#     Bsbrood  (number of broods)
#
# The effect of xi[i,j] on eta[i,1] is included by the regression coefs gam1.i
# The effect of latent variable on each other is included in the regression coef gamj.i
# For each latent variable, one of the loading factor is set to 1.

## specify model
sink("sem.bug")
cat("
   model{

   for (i in 1:N){   # for each focal individual
   ## measurement equation model
   for (j in 1:L){   # for first set of continuous variables (associated with fixed laoding factor)
   y[i,j] ~ dnorm(mu[i,j], psi[j])
   epshat[i,j] <- y[i,j]-mu[i,j]     # unexplained residuals
   }
   for (j in (L+1):(L+P)){    # for each ordered categorized variable
```

```
  y[i,j] ~ dnorm(mu[i,j], psi[j])I(thd[j,z[i,j]], thd[j,z[i,j]+1])
  epshat[i,j] <- y[i,j]-mu[i,j]     # unexplained residuals
  }
  for (j in (L+P+1):V){    # for the other continuous variable
  y[i,j] ~ dnorm(mu[i,j], psi[j])
  epshat[i,j] <- y[i,j]-mu[i,j]     # unexplained residuals
  } # end of j


  for (j in 1:V){    # for computing bayesian p-value
  y.new[i,j] ~ dnorm(mu[i,j], psi[j])              # simulation of data
  E.org[i,j] <- pow((y[i,j]-mu[i,j]),2)/mu[i,j]      # chi2 between observed (y) and expected data (mu)
  E.new[i,j] <- pow((y.new[i,j]-mu[i,j]),2)/mu[i,j]  # chi2 between simulated (y.new) and expected data (mu)
  }

  # Previous breeding xi[i,1]
  mu[i,1] <- lam[1]*xi[i,1]    # Pfledg1 - number of fledglings = 1
  mu[i,7] <- lam[7]*xi[i,1]    # Pbrood

  # Fall migration xi[i,2]
  mu[i,2] <- lam[2]*xi[i,2]   # FaDep - Departure for fall migration;lam fixed to 1
  mu[i,9] <- lam[9]*xi[i,2]   # FaDur - Duration of fall migration

  # Winter timing xi[i,3]
  mu[i,3]  <- lam[3]*xi[i,3]   # WiArr - Arrival on Wintering ground;lam fixed to 1
  mu[i,10] <- lam[10]*xi[i,3]  # WiDur - Duration of wintering

  # Winter condition xi[i,4]   # winter period: October -> Feb
  mu[i,4]  <- lam[4]*xi[i,4]   # WiNDVI_median - overall greeness of the area for the wintering period
  mu[i,11] <- lam[11]*xi[i,4]  # WiNDVI_delta - (median value for Feb - median value for Oct)

  # Spring migration xi[i,5]
  mu[i,5]  <- lam[5]*xi[i,5]   # SpDep - Departure for spring migration ; lam fixed to 1
  mu[i,12] <- lam[12]*xi[i,5]  # SpDur - Duration of sprign migration

  # Breeding success eta[i] - to be explained
  mu[i,6] <- lam[6]*eta[i]   # Bsfledg1 - number of fledglings ; fixed to 1
  mu[i,8] <- lam[8]*eta[i]   # Bsbrood

  ## structural equation model
  eta[i] ~ dnorm(nu[i], psd[1])
  nu[i]   <- gam1[1]*xi[i,1]+gam1[2]*xi[i,2]+gam1[3]*xi[i,3]+gam1[4]*xi[i,4]+gam1[5]*xi[i,5] # direct effect on
breeding success of previous breeding (xi[1]) and Spring mig (xi[5])
  dthat[i] <- eta[i]-nu[i]     # unexplained residuals

  eta.new[i] ~ dnorm(nu[i], psd[1])

  xi[i,5] <- gam5[1]*xi[i,4] + gam5[2]*xi[i,3] + eps[i,5] # direct effect on Spring migration
  xi[i,4] <- gam4*xi[i,2] + eps[i,4]                  # direct effect on Winter Condition
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```
xi[i,3] <- gam3*xi[i,2] + eps[i,3]              # direct effect on Winter timing
xi[i,2] <- gam2*xi[i,1] + eps[i,2]              # direct effect on Fall migration
xi[i,1] <- eps[i,1]
eps[i,1:5] ~ dmnorm(u[1:5], phx[1:5,1:5])

} # end of i = each focal individual


fit <- sum(E.org[,])      # sum of chi2 between observed (y) and expected data (mu)
fit.new <- sum(E.new[,])  # chi2 between simulated (y.new) and expected data

for (j in 1:5){
        u[j] <- 0.0
        }

### priors on laodings and coefficients
## loading factors
for (j in 1:L){
lam[j]<-1.0
}
for (j in (L+1):V){ # for each lambda
lam[j] ~ dnorm(0.8, var.lam[j])
}  # end for lambda
# loading factor variance
var.lam[7]  <- psi[7]    # loading factor Pbrood <- xi[1]
var.lam[8]  <- psi[8]    # loading factor Bsbrood <- eta[1]
var.lam[9]  <- psi[9]    # loading factor FaDur <- xi[2]
var.lam[10] <- psi[10]   # loading factor WiDur <- xi[3]
var.lam[11] <- psi[11]   # loading factor WiNDVI_delta <- xi[4]
var.lam[12] <- psi[12]   # loading factor SpDur <- xi[5]
for (j in 1:V){ # for each psi
psi[j] ~ dgamma(10,8)
sgl[j] <- 1/psi[j]
}  # end of psi


## regression coefficient
for(i in 1:5){
gam1[i] ~ dnorm(0, var.gam1) # reg coef on BS
}
for (i in 1:2){
gam5[i] ~ dnorm(0, var.gam5) # reg coef on Spring migration
}
gam4 ~ dnorm(0, var.gam4) # reg coef of Fall migration on Winter condition
gam3 ~ dnorm(0, var.gam3) # reg coef of Fall migration on Winter timing
gam2 ~ dnorm(0, var.gam2) # reg coef of Previous breeding on Fall migration
# variance or reg coef
var.gam1 <- psd[1]
var.gam5 <- psd[5]
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```
   var.gam4 <- psd[4]
   var.gam3 <- psd[3]
   var.gam2 <- psd[2]
   for (x in 1:5){
   psd[x] <- 1/sgm2[x]
   sgm2[x] <- sgm[x]*sgm[x]
   sgm[x] ~ dunif(0.0001,10)
   } # end of psd

   # covariance between exogenous latent variables
   phx[1:5,1:5] ~ dwish(R[1:5,1:5],5)
   phi[1:5,1:5] <- inverse(phx[1:5,1:5])  # covariance matrix of xi[j]

   }
   ",fill=T)
sink()

## Data
R <- diag(5)
bugs.data <- list (y=data.sem,z=data.sem,thd=thd,N=N,V=V,P=P,L=L,R=R)

## Initial values   ## for inits, don't use "<-" but "="
inits <- function(){
  list(lam  = c(rep(NA,L),1.2,1.0,1.1,0.5,-0.5,-0.7),
      gam1 = c(rep(0,5)),
      gam5 = c(rep(0,2)),
      gam4 = 0,
      gam3 = 0,
      gam2 = 0,
      sgm = c(rep(1,5)),
      eps = matrix(0, ncol = 5, nrow = N))
}

## Parameters monitored
parameters <- c("lam","sgl","gam1","gam5","gam4","gam3","gam2","sgm","phi","fit","fit.new")

## MCMC settings
ni <- 100000  # nb of iterations
nt <- 3       # nb of thinning
nb <- 50000   # nb of burnin
nc <- 5       # number of chains of Monte Carlo

## load libraries
library(MASS)      #Load the MASS package
library(R2WinBUGS) #Load the R2WinBUGS package
library(boa)       #Load the boa package

## starting point
start <- Sys.time()
```

```
## Call WinBUGS
sem <- bugs(data=bugs.data, inits=inits, parameters.to.save=parameters, model.file="sem.bug",
        n.chains=nc, n.iter=ni, n.burnin=nb,n.thin=nt,DIC=T,digits=5,
        bugs.directory="D:/WinBUGS14",debug=F)

## Ending point
end <- Sys.time()

## Duration
duration <- end - start  # duration of computation
duration

# Show results
print(sem,digits=3)

## posterior distribution check
# gam1[1]
plot(density(sem$sims.list$gam1[,1]),main="",frame=F,xlab=expression(gamma[1.1]))
abline(v=sem$mean$gam1[1],col="red")
# gam1[2]
plot(density(sem$sims.list$gam1[,2]),main="",frame=F,xlab=expression(gamma[1.2]))
abline(v=sem$mean$gam1[2],col="red")
# gam1[3]
plot(density(sem$sims.list$gam1[,3]),main="",frame=F,xlab=expression(gamma[1.3]))
abline(v=sem$mean$gam1[3],col="red")
# gam1[4]
plot(density(sem$sims.list$gam1[,4]),main="",frame=F,xlab=expression(gamma[1.4]))
abline(v=sem$mean$gam1[4],col="red")
# gam1[5]
plot(density(sem$sims.list$gam1[,5]),main="",frame=F,xlab=expression(gamma[1.5]))
abline(v=sem$mean$gam1[5],col="red")
# gam5[1]
plot(density(sem$sims.list$gam5[,1]),main="",frame=F,xlab=expression(gamma[5.1]))
abline(v=sem$mean$gam5[1],col="red")
# gam5[2]
plot(density(sem$sims.list$gam5[,2]),main="",frame=F,xlab=expression(gamma[5.2]))
abline(v=sem$mean$gam5[2],col="red")
# gam4
plot(density(sem$sims.list$gam4),main="",frame=F,xlab=expression(gamma[4]))
abline(v=sem$mean$gam4,col="red")
# gam3
plot(density(sem$sims.list$gam3),main="",frame=F,xlab=expression(gamma[3]))
abline(v=sem$mean$gam3,col="red")
# gam2
plot(density(sem$sims.list$gam2),main="",frame=F,xlab=expression(gamma[2]))
abline(v=sem$mean$gam2,col="red")
```

```
## Bayesian p-value  value should be close to 0.5
mean(sem$sims.list$fit<sem$sims.list$fit.new)

## save the coef
sink("result.sem.txt")
print(sem,digits=3)
cat("
   ## Bayesian p-value  value should be close to 0.5
   mean(sem$sims.list$fit<sem$sims.list$fit.new)
   0.4865063

   ### probability that the coef are strictly positive/negative
   # the probability is based on the result from the MCMC sample

   ### direct effect on breeding success
   ## From Previous breeding (gam1.1)
   mean(sem$sims.list$gam1[,1]>0)
   # 0.9699406
   ## From Fall mig (gam1.2)
   mean(sem$sims.list$gam1[,2]>0)
   # 0.4733425
   ## From Winter Timing (gam1.3)
   mean(sem$sims.list$gam1[,3]>0)
   # 0.3814244
   ## From Winter Cond (gam1.4)
   mean(sem$sims.list$gam1[,4]>0)
   # 0.4129237
   ## From Spring mig (gam1.5)
   mean(sem$sims.list$gam1[,5]>0)
   # 0.5626567

   ### effect between latent variables
   ## Winter Condition -> Spring (gam5.1)
   mean(sem$sims.list$gam5[,1]>0)
   # 0.6235435
   ## Winter Timing -> Spring (gam5.2)
   mean(sem$sims.list$gam5[,2]<0)
   # 0.700366
   ## Fall -> Winter Condition (gam4)
   mean(sem$sims.list$gam4>0)
   # 0.7102778
   ## Fall -> Winter Timing (gam3)
   mean(sem$sims.list$gam3>0)
   # 0.8640067
   ## Previous -> Fall (gam2)
   mean(sem$sims.list$gam2>0)
   # 0.5068099
   ")
sink()
```

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March 2012 – Jan 2016 **PhD thesis** at the Swiss Ornithological Institute & Department of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

2008-2010 **M.Sc. Biology**, specialization ***Ecology***, minor *Geo-Information Science* at Wageningen University, The Netherlands. Graduated 21st of October 2010

2010 **MSc Thesis** on nest predation characteristics of the Grasshopper buzzard *(Butastur rufipennis)* in the Extreme North of Cameroon. *See publications*

2010 **MSc research internship** on testing the Green wave hypothesis for White Fronted Geese (*Anser albifrons*) within an internship at The Netherlands Institute for Ecology (NIOO-KNAW). *See publications*

2009 **MSc Thesis** on the movement characteristics of the Common hamster (*Cricetus cricetus*) in Limburg, the Netherlands. *See publications*

2005-2009 **B.Sc. Biology (*Ecology*)**, finished 19th of March 2009. BSc thesis "Dispersal of mammals in the field of animal ecology – differences between small and large mammals"

1999-2005 Gymnasium (highest level of secondary education) at Bogerman College in Sneek, the Netherlands

Publications (other than chapters of this thesis)

Van Oosten, H., Versluijs, R. and **van Wijk, R. E.** 2014. Migration routes and wintering areas of two Dutch Northern Wheatears Oenanthe oenanthe in the Sahel. - Limosa 87: 168–173.

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Presentations and Courses

August 2013 - Presentation at the European Ornithological Union (EOU) Conference entitled "*Lessons from huge variation in migration patterns in Eurasian Hoopoes Upupa epops and its potential consequences for general concepts in bird migration*"

February 2014 – Presentation at the Netherlands Annual Ecology Meeting entitled "*Opportunistic tracking of food resources in the northern Sahel: plasticity in migratory behaviour of a Palaearctic-African bird species*"

August 2015 - Presentation at the EOU conference entitled "*The timing of migration in a Palaearctic-African migrant and its consequences on reproductive success*" plus co-organizer of the satellite symposium "*Connecting migrant landbird research and conservation across the flyway*"

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